STUDIES OF RECRUITMENT IN THE GREAT SKUA

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Candidate's declaration

I declare that the work described in this thesis has been carried out by myself, unless otherwise stated. It has not been, in whole or in part, submitted for any other degree.

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Abstract

Recruitment is a major determinant of population dynamics in long-lived animals. In most seabird colonies it is common to find groups of immature birds gathering near territories waiting to recruit. The process of recruitment is affected by individual quality but also by environmental conditions and colony density. The state of the pool of potential recruits could be a sign of the health of a population, changes in numbers of non-breeders can give cues of the future of the colonies. This thesis examines different variables affecting recruitment, and provides evidence of recent events affecting a seabird colony. Fieldwork was conducted during 2003-05 in the island of Foula, Shetland. Foula holds the largest colony of great skuas *Stercorarius skua* in the world; although numbers of breeding pairs in the colony increased rapidly from 1900-70, recently numbers have been decreasing. Data were collected by marking non-breeders and taking individual measures, individuals were followed in subsequent seasons to record their behaviour. An extended database was used to determine how long-term effects of variables such as hatching date, food availability and climate change affect the process of recruitment. The results show that food availability is related to breeding success and early hatching, as well as the probability of returning to the colony to breed. The variable used to quantify climate change (NAO winter index) was not related to recruitment, however it is suspected to influence food abundance. Contrary to expectation, individual quality did not have an effect on the probability of breeding for the first time, and there was no difference in body condition between potential recruits and established breeders; however historic data suggest a difference. The current situation faced by great skuas in the Foula colony may be a determinant for the changes in recruitment rates as well as for the parameters that determine the recruitment process. Compared to two decades ago, numbers of pre-breeders have decreased substantially which may give evidence of density dependent effects preventing the addition of new recruits to the colony.

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I dedicate this thesis to my parents and to my husband for all their love and support, because it means everything to me.

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1. General Introduction

1.1 Colonial Breeding in Seabirds

The reason why animals form colonies has always intrigued biologists, the immediate assumption is that individuals must benefit in some way from nesting so close to conspecifics, however the study of colonial breeding shows that these benefits are also counterbalanced by some disadvantages. Overall, the exposure to conspecifics provides the opportunity of information exchange (i.e. foraging, mating), which in turn saves individuals potential waste of time that could affect their fitness (Nelson 1980). More than 95% of all seabirds breed in colonies, it is a wide spread phenomenon amongst different species and it is present in all latitudes regardless of individual size and habitats (Nelson 1980). Coloniality increases social interaction, with benefits such as social stimulation and breeding synchrony which suggests that individuals can adjust to a specific time of breeding corresponding to adequate environmental conditions (Coulson 1983, 2002). Other benefits may include social awareness of predators and information about food sources; maximum colony size is dependent on foraging range and food availability (Nelson 1980, Coulson 2002). However, it has been discussed that breeding in close proximity to other birds holds some problems: easier transfer of parasites and diseases may occur, as well as higher aggression leading to intraspecific predation (Nelson 1980; Coulson 2002). At the same time there are density dependent effects and higher competition for food and mating partners amongst individuals (Nelson 1980; Coulson 2002). But colonial breeding has evolved separately in many occasions which indicates that it is an adaptive process, some hypotheses have been proposed to explain the benefits of this behaviour (Danchin and Wagner 1997; Coulson 2002). The advantages of colonial breeding may include nesting in a place relatively free of predators like a sea cliff or an island, and it provides the opportunity to socially interact with conspecifics. Seabird breeding colonies are located close to good feeding grounds and it could be possible to think that this kind of sites are limited and therefore birds have to breed in large groups. The choice of nesting on a colony could be based on the presence of conspecifics in the

site and their reproductive success, named the "Commodity Selection" hypothesis, this explains that individuals are attracted to certain sites by conspecifics which may give them cues about the nesting habitat, it also involves sexual selection because in the same way individuals select "reproductive commodities" like mating partners and even extra-pair copulations (Danchin and Wagner 1997, 1999).

The social arrangement of colonial breeding restrains some individuals from nesting in all available spaces (more or less dense areas), there is a ranked distribution of breeding spaces amongst colony sites. Usually, older birds occupy central (desirable) sites, whereas young breeders are left with territories at the edges of the colony which are not socially accepted (Coulson 2002). Colony density can enhance competition for nesting sites and raise the number of non-breeding birds in the population; and at the same time increase the age at which individuals start to breed; in dense colonies the expected age of first reproduction is greater than in less populated colonies (Chabrzyk and Coulson 1976; Coulson 2002). In a colony, new recruits have the opportunity to take vacant spaces in privileged sites of the colony if previous breeders have not returned, although most of them are already occupied so they are generally restricted to lower quality sites (Coulson 2002).

1.2 Recruitment

The addition of individuals to a breeding population is known as recruitment; these new breeders are birds who may have been born in the same population or that have come from elsewhere (Danchin et al. 1991; Oro and Pradel 2000). Recruitment and the age of recruitment are important determinants of population dynamics, being related to population numbers and emigration/immigration rates (Oro and Pradel 2000). The process of recruitment is influenced by several physiological, social and environmental factors, such as age, colony size and density, body condition and food availability. After reaching an adequate age for breeding, birds have to choose the most suitable place to nest, at this point

they are faced with the decision of choosing their natal colony or to immigrate into another colony. At this stage individuals will assess different colonies in order to choose the most suitable place to breed (see prospecting in 1.2.2). It has also been mentioned that there is variation in the "quality" of the potential recruits, and that individual condition plays an important role at the time of recruitment (Porter and Coulson 1987). The so called "pool of potential recruits" is an indicator of the state of a colony, a decrease in the number of prospecting non-breeders may be an indicator of a decline of the population (Porter and Coulson 1987, Klomp and Furness 1992).

1.2.1 Age at first breeding

The age at which different seabird species start to breed varies widely. Before breeding for the first time individuals are regarded as immatures. The period of time before first reproduction is thought to be for acquiring all the relevant social skills as well as the physiological condition to breed. In many cases birds need to obtain complex foraging skills and reproductive displaying techniques which are necessary for successful breeding (Furness and Monaghan 1987; Bradley and Wooller 1991). Some determinants of the age at first breeding are the complexity of the feeding methods and the availability of food; others are aspects of life history like longevity and fecundity, with which age at first breeding correlate closely (Nelson 1980). Seabirds have a relatively low adult mortality and do not breed in the year following their birth, also they may spend prolonged periods of time before reproducing (Bradley and Wooller 1991; Bradley et al. 1999). In some species there are differences in age of first breeding between males and females and these are related to survival rates and reproductive effort (Wooller and Coulson 1977). Some examples of age at first breeding include wandering albatrosses (*Diomedea exulans*) who breed at the average age of 10, the same as royal penguins (*Eudyptes schlegeli*); on the other hand atlantic gannets (*Morus bassanus*) breed at a younger age (4-5 years old), cape gannets (*Morus capensis*) at 2-3 years old, herring gulls

(*Larus argentatus*) between 3 and 4 and sooty terns (*Sterna fuscata*) at around 6 years of age (Nelson 1980).

Younger birds have comparatively lower reproductive success. Thus breeding at a younger age does not necessarily increases lifetime reproductive success; if breeding effort also affects future prospects in terms of survival rate or prospects for future breeding, the decision of when to start breeding is a trade-off between current and future reproductive success (Furness and Monaghan 1987; Bradley and Wooller 1991). These ideas have been summarized into two hypotheses: the "constraint hypothesis" which suggests that individuals are prevented from breeding by social and endocrinological factors; and on the other hand the "restraint hypothesis" which proposes that birds delay breeding to avoid excessive future reproductive costs (Curio 1983; Oro and Pradel 2000). Recruitment age may vary in response to the current state of a population (i.e. depending on limiting factors such as food availability and nesting space); when resources are limited and there is a high density of birds, productivity decreases and breeding age may increase, the opposite could also be expected (Nelson 1980).

1.2.2 Prospecting before breeding

In seabird colonies it is common to find birds that are actively looking for a nesting space, many of them would be immatures but others may be individuals that have previously bred somewhere else in another colony or within the same colony and either lost their mate or divorced (Danchin et al. 1991). They are known as *prospectors* and evidence suggests that they visit different places before deciding where to nest, either visiting different nest sites within a colony or visiting a variety of different colonies. Immatures usually arrive to the colonies earlier in the season and attend more frequently as they become older, Halley et al. (1985) showed that new recruits had been seen more times in the season prior to breeding than non-breeders; at the same time they showed that younger common guillemots (*Uria aalge*) visited more colonies before their first breeding

(Halley et al. 1995). Individuals are presumed to use prospecting as a method of gathering information about the quality of the breeding habitat, therefore they spend time testing different colonies/nesting grounds before choosing where to settle (Boulinier and Danchin 1997; Boulinier et al. 1999). Some evidence of the use of conspecific information has been given by studies with kittiwakes (*Rissa tridactyla*) in a colony in Brittany, France, where attendance by prospecting birds was greater in more successful colonies and where breeding success was related to recruitment rates, giving evidence that prospectors evaluate local reproductive success and quality of the colony before breeding (Cadiou 1999). Similarly, in great cormorants (*Phalacrocorax carbo*) it was found that conspecific reproductive success affects recruitment age, in this species age at first breeding increased in years of low reproductive success (Frederiksen and Bregnballe 2001). Prospectors tend to arrive later than established breeders; experienced non-breeders in better body condition arrive earlier than younger birds, giving them more opportunity to obtain suitable nests (Dittmann and Becker 2003). In some species there are differences between the sexes in arrival to the colony and frequency of visits, usually males have to defend territories, so early arrival could be more important for them than for female recruits (Nelson 1980; Dittmann and Becker 2003).
Prospecting has also been recognized in other bird species such as collared flycatchers (*Ficedula albicollis*) where individuals are attracted to sites with high reproductive success (Doligez et al. 2004; Part and Doligez 2003). In common loons (*Gavia immer*) prospectors frequently visit sites with chicks supporting the idea of "habitat copying" which could eventually lead to a territory takeover (Piper et al. 2006). Birds would prospect before breeding in search for "public information", although it is not entirely understood which cues allow them to make the decision of choosing a nest (other examples: bobolinks, *Dolichonyx oryzivorus*, Nocera et al. 2006; yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, Ward 2005).

1.3 Philopatry

The term "philopatry" is used when individuals return to breed at the place they were born. Seabirds usually migrate away from their breeding areas each year and it seems to be adaptive for young birds to return to their natal place to reproduce (Nelson 1980; Bradley and Wooller 1991). Once they have established as breeders in a particular colony they show high tenacity and fidelity to the site and it is very likely that they will return for most of their subsequent breeding attempts to that place (Furness and Monaghan 1987). However, these observations do not signify that they would not visit other colonies, in fact as previously mentioned birds prospect in different places before deciding where to settle. Although the natal colony could be the preferred option, other factors may affect the decision of being philopatric; for example when there is high competition for resources in the natal site. Recruiting into a particular area depends on colony size, overall reproductive success and food availability (Oro and Pradel 2000). So, philopatry is not always the case in all species and often there is movement between colonies; a bird would make the decision of breeding elsewhere (i.e. emigrating) before breeding for the first time (Chabrzyk and Coulson 1976; Coulson and Demevergnies 1992). The balance between philopatry and emigration, and the balance between visiting only the natal colony and visiting a wide range of colonies probably varies among seabird species according to aspects of species' ecology, but the extent to which these patterns vary between species or in different environmental conditions (see the next section of this chapter) is not well known. The majority of recruitment occurs in colonies that are already formed. Colonizing of new sites takes place after years of visits to other places and it usually requires a few pairs to start breeding for the colony to grow (Coulson 2002).

1.4 Factors affecting recruitment

The recruitment rate is affected by different variables, one of them is colony size. A change in density of a colony can affect the age at first breeding; for example in herring gulls (*Larus argentatus*), after a reduction in population numbers, more young birds (3 years old) were recorded breeding than before the population reduction (Coulson et al. 1982). In another study about local recruitment in the Audouin's gull (*Larus audouinii*) it has been shown that the probability of any individual to breed increased with the size of the colony. At this site, the breeding numbers were growing dramatically and this meant that recruitment occurred at a younger than average age (Oro and Pradel 2000). On the contrary, in the Cassin's auklet (*Ptychoramphus aleuticus*) the age at first breeding increased when density in the colony was low (Pyle 2001). The other reason explaining their results was low food supply, therefore that was also related to the increase in age at first reproduction. Environmental variables are also related to the recruitment process, climatic events like "El Niño" have been related to recruitment age (Spear et al. 1995); and more recently climatic change has been associated with low breeding success and recognized to affect recruitment in different animal species. Food abundance is also associated with recruitment numbers, as could be expected there are low numbers of recruits when food supply is low (Boekelheide and Ainley 1989; Spear et al. 1995).

Also, evidence suggests that in some seabird species there is a selection of individuals at the time of recruitment based on the quality of the potential recruits (Wooller and Coulson 1977). This selection is based on individual body condition, levels of colony attendance and age, as well as site tenacity and time of arrival to the colony (Porter 1988). The variation in the quality of prospecting non-breeders determines where and when the birds will nest, higher quality birds appear to nest in dense areas due to their ability to defend the territory even against previously established breeders (Porter 1990). From the pool of potential recruits, the ones that

arrive later would have to remain in the non-breeding pool, early birds that are not fit enough will also remain in the pool whereas high quality birds would recruit; however individuals in better condition would take the best nesting spaces (Porter 1990).

Recruitment rate is an element of population dynamics, in conjunction with mortality and emigration rates they shape population sizes. Recruitment can regulate seabird populations determining declines in numbers or growth (Furness and Monaghan 1987). Studies of recruitment provide valuable information about seabird populations that could be useful for monitoring, control or conservation purposes (Furness and Monaghan 1987).

1.5 Studying recruitment

Recruitment rate is one of the most important components of population dynamics along with mortality and reproductive success. However the study of recruitment has had little attention over the years. It is until recently that long-term data sets have been used to study recruitment. Long-term studies in which birds have been ringed as chicks give the opportunity to follow up with their life history, it is possible to establish whether they returned to the same colony to breed or potentially determine if they bred elsewhere. To deal with the recruitment information statistically, different models have been developed (Pradel and Lebreton 1999); the most commonly used is the mark-capture-recapture model in which the life of an individual is read "backwards" from the moment it was last seen to the moment it first bred (Pradel 1996). Pradel and Lebreton (1999) also suggest another model in which one can predict when an individual would breed based on a "non-observable" state. However most of the studies dealing with recruitment consider the individual only when it starts breeding, there are not many studies about the behaviour and conditions experienced by pre-breeders in the years before acquiring a territory. As mentioned before, seabirds usually return to their colonies after their first year and they visit the colonies frequently in order to interact with conspecifics, but during this period it is not always possible to trap them or to obtain any

information about them. Studies like the present thesis are valuable because they provide individual information of the period before the first reproduction. However, the data obtained in this study did not allow a model analysis; the sample size is small (not all the birds captured as non-breeders/prospectors had been ringed as chicks) and there are not many encounters registered. Also it would be ideal to have a large data set including several years of "recapture" observations.

1.6 Great Skuas as study species

Great skua (*Stercorarius skua*) breeding range is restricted to the North Atlantic, the largest number of breeding pairs are located in Iceland and North Scotland (Shetland and Orkney Islands)(Furness 1987). Great skuas like most seabirds are monogamous, long-lived and highly site faithful as breeders, they also tend to defend their territories very aggressively against conspecifics, other animals and even humans. Before recruiting, they gather in easy identifiable locations amongst territories of the breeding colony to perform social interactions with conspecifics (Klomp and Furness 1992; see Chapter 4). They are able to exploit a wide variety of food sources depending on their location, although in northern Scotland they mainly forage on sandeels and fisheries discards (Furness 1987; Votier et al. 2003). The total population has increased in the past decades and now stands at around 16000 pairs, most of which breed in Britain (Furness and Ratcliffe 2004). Recently there have been reports of a decrease in numbers of birds in large colonies and an increase of breeding pairs in smaller colonies, suggesting a certain degree of density dependent competition for food (Furness and Ratcliffe 2004).

Although there have been studies about non-breeding great skuas in the past (Klomp and Furness 1990, 1992), there is not enough information about recruitment or comparisons with breeding birds. But, it is known that breeders and non-breeders have a similar diet from pellet analysis of samples collected around the colony, in breeding territories and club-sites (Votier et al. 2001). Also it is known that young birds migrate to different

regions than adult birds; 18-24 month old great skuas travel to America (North America and Caribbean), Scandinavia, South Europe and North West Africa, whereas adults migrate to Southern Europe and North West Africa (Furness 1987). In terms of activity during the breeding season, breeders attend only one colony whereas non-breeders could potentially visit several colonies whilst prospecting. Knowing the differences and similarities between breeders and non-breeders could help to understand the conditions they are subject before arrival to the colony and during the breeding season. These elements could affect individual traits such as body condition (both breeders and non-breeders) and the choice of a nesting place (non-breeders).

For experimental purposes it is advantageous to find non-breeders gathering in these big groups because it allows trapping and marking of individuals that can be followed in coming seasons. This species is ideal to study recruitment, because it gives the opportunity to have a record of behaviour and body condition of the birds before breeding. Therefore it is possible to relate different variables to the probability of recruitment.

1.7 The Foula Colony

The island of Foula (60°08'N 2°05'W) is located west of Shetland mainland in the north of the British Isles. This small but inhabited island holds large colonies of different seabird species that nest all over the moor in the mainland and around the sea cliffs. One of the most common seabird visitors breeding on the moors/grasslands of the island is the great skua or "bonxie" as it is called locally, which during the reproductive season occupies vast areas of the island. Foula holds the largest population of great skuas in the world, which had a rapid growth in the last century (Furness 1987), more recently the number of breeding pairs have been declining from 2495 apparently occupied territories (AOT) in 1985-86 to 2293 AOTs in 2000 (Furness and Ratcliffe 2004). Since the 1970s there has been annual monitoring of the breeding colony which has included ringing and measuring of both chicks and adult birds, this has facilitated the study

of the colony providing individual information like age, breeding status and in some cases body condition. There has been a long tradition of research into great skua ecology by postgraduate students and research fellows, from the PhD thesis by Bob Furness in 1977 through a continuous series of researchers to the end of the 20th century. This research provides both a good understanding of the ecology of this population, and also a long time series of data that can be related to aspects of changing environmental conditions (e.g. Votier et al. 2004). Despite this detailed and extensive research programme, only one PhD student considered the numbers and behaviour of non-breeding great skuas as a significant part of his PhD research (Klomp and Furness 1992), and there has been no further work on this topic since that time.

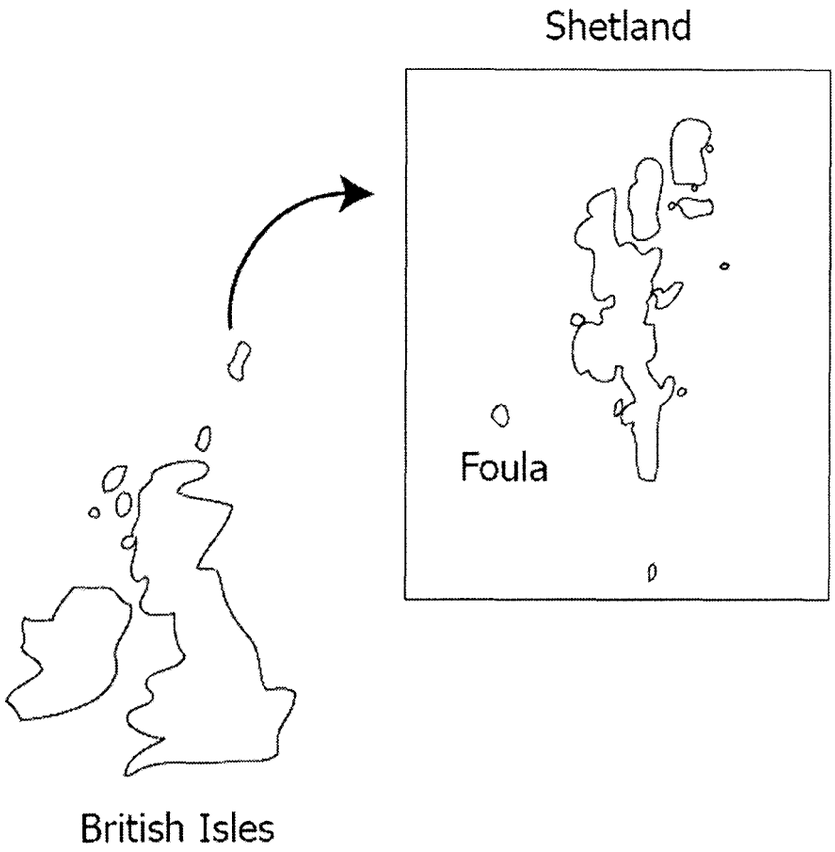


Figure 1.7.1 Geographical location of Foula, Shetland.

1.8 Outline of the thesis

The current status of the breeding colony of Great Skuas in Foula provides an excellent opportunity to study aspects of seabird population dynamics. The aims of this study are to understand better the process of recruitment and to consider previous ideas in the current context of this population, with the use of recent and previously collected data.

Chapter 2 examines how reproductive variables (and particularly hatch date) are affected by environmental factors such as climate change and food availability, also it analyses the effects of these variables (climate change and food availability) on survival and recruitment. Results include somewhat sporadic accumulated data from both breeders and non-breeders taken in previous years, as well as data specifically collected on these issues in the time of this study. In order to test the idea that recruits need to achieve a certain level of body condition as a "pre-requisite for recruitment" (Porter 1988), in **Chapter 3**, I analysed the differences in body size and condition between breeders and non-breeders. It is important to evaluate the conditions faced by new breeders, especially in a highly dense colony like Foula.

As mentioned before, pre-breeders visit colonies in order to assess their quality before nesting, so in **Chapter 4**, I look at the attendance patterns of non-breeders in the colony and its relationship to time and date; also there is a comparison between the numbers of non-breeders present in the Foula colony amongst the years of this project and with reports of previous similar studies particularly those by Nick Klomp over a decade ago. This chapter draws attention to the importance of the number of potential recruits to the status of the colony, and the relationship between non-breeders and population numbers. In the final data chapter (**Chapter 5**), the results of three years of observations are shown; I investigate how body condition during the breeding season could affect the fate and status of potential recruits from one year to the next. This chapter discusses the

possibilities of birds breeding in Foula as opposed to emigrating to another colony. In the final discussion, I summarize the findings of this project and evaluate the objectives, explaining the development of the study and its importance for conservation biology.

2. Environmental factors affecting breeding and recruitment

2.1 INTRODUCTION

2.1.1 Hatching date and survival

There is a large variation in the survival rates of birds during their lifetime, and it tends to be lower after fledging and during the first year of their lives than as adults (Dunn 1972). Survival of an individual from hatching to recruitment is influenced by several different factors, including physiological traits as well as challenging environmental conditions faced through that period. However, evidence shows that the timing and conditions at hatching are crucial for young birds in order to reach maturity. Parental ability to produce quality eggs, and care for chicks has proven to be an important factor affecting post fledging survival. It is known that laying earlier in the season is beneficial in terms of higher reproductive success, so there is a preference of early laying by the parents (Drent and Daan 1980; Price et al. 1998; Dawson and Clark 2000). Also, in seasonal environments parents will adjust breeding to match peak food availability, thus increasing the chances of survival of their young (Catry et al. 1998). In a study on the breeding biology of common guillemots (*Uria aalge*), Wanless and Harris, found that early hatched chicks had significantly longer fledging periods than late chicks, and that the timing of breeding had a significant effect on the breeding success of the colony in general (Wanless and Harris 1988). Other studies have recognized the importance of hatching date on chick growth and fledging success. Birds breeding earlier in the season hatched in better condition than late-hatched individuals and have higher survival probabilities (e.g. Sedinger and Flint 1991; Arnold et al. 2004). Spear and Nur conducted a study in which they tested the effects of different reproductive variables (brood size, hatching order, hatching date, fledging weight) on different life stages of Western gulls (*Larus occidentalis*). They found a strong negative effect of hatching date on survival; the probabilities of surviving the three different stages of age (natal, juvenile and recruitment) were reduced for late hatched chicks (Spear and Nur 1994). Hatching date has also been

related to competitive ability and breeding strategies in seabirds. Early hatched individuals start breeding at a younger age and show dominant behaviours over their conspecifics (magpies (*Pica pica*): Eden 1987; shags (*Phalacrocorax aristotelis*): Velando 2000; black-headed gulls (*Larus ridibundus*): Prevot-Julliard et al. 2001).

Is hatching date related to recruitment?

Assuming that hatching date has an effect on post-fledging survival, and that early fledged chicks have an advantage over late fledged chicks, we could assume that there is a relationship between hatching date and the probability of recruitment into the breeding population. The benefits of early hatching are reflected in better body condition, which in turn signifies greater ability to compete for breeding spaces. Cooke et al. (1984) found that early-hatched lesser snow geese (*Anser c. caerulescens*) chicks had significantly greater recruitment rates than late hatched chicks. Although the tendency was present in all seasons they recorded, significant results were season-dependent. Similar results were found in the lesser scaup (*Aythya affinis*) by Dawson and Clark (2000), where recruitment probability also decreased among birds with later hatching dates. It is possible that the reason for low recruitment in late-hatched individuals was related to the time available to acquire nutrients for migration, thus late-hatched birds had increased mortality rates (Dawson and Clark 2000). In black-headed gulls (*Larus ridibundus*), Prevot-Julliard et al. (2001) found that even a few weeks' difference in hatching date between chicks has an effect later in life; chicks hatched earlier started breeding younger, and later hatched birds were found breeding on peripherial colonies. Considering these results, it is reasonable to expect a strong correlation between hatching dates and the probability of recruitment into the breeding populations.

Great Skuas

Since 1975, Great Skua chicks have been ringed and measured in large numbers each year in Foula, Shetland. During the early 1980s there was a tendency for early breeding, while breeding was later in the late 1980s when sandeel abundance was low and breeding success was reduced (Furness 1987). This suggests a relationship between food availability and laying/hatching date.

Breeding success of great skuas declines with laying date, later breeders have only approximately 25% chance of producing fledglings. Success is related to parental quality, later laying birds are usually inexperienced birds. Southern hemisphere (Sub Antarctic) skuas seem to time their breeding with seasonal patterns that relate to latitude and climate, and presumably also to the time of peak food availability (Furness 1987), but there has been no analysis of the factors affecting timing of breeding of great skuas. Early hatched chicks have higher post-fledging survival, probably because they have larger body reserves. However, the effect of hatching date on survival of great skuas does not extend beyond the first year, and it is not related to subsequent timing of breeding. In a study conducted in the Foula colony from 1975 to 1990, Catry et al. found a significant effect of hatching date on survival probability in the first year, and also early hatched chicks had on average, a better body condition than late hatched chicks (Catry et al. 1998).

2.1.2. Environmental variables that affect hatching date and recruitment

Food Availability

Food availability has been associated to overall breeding performance. In great skuas an improved availability of sandeels was related to earlier laying dates, possibly as a consequence of females in better condition to lay eggs (Ratcliffe et al. 1998). Early laying may present selective

advantages in terms of fledging success and reduced intraspecific predation.

Some studies have recognized the effect of environmental conditions on the survival of individuals to recruitment age; these effects have a stronger impact on the life histories of individuals in seasonal environments (Reed et al. 2003). Environmental changes affect directly the food availability, and these effects turn out to be stronger for less experienced birds. In Western gulls, when food availability is reduced, mature birds tend to breed earlier than younger birds, therefore hatching chicks earlier and producing more fledglings (Sydeman et al. 1991).

It is thought that animals would adjust the time of breeding to the time when food availability is higher in order to provide the energetic demands of reproduction and chick rearing. Individuals rely on physiological and climatic cues to make the decision of when to start breeding in any particular year. This is mostly important to animals that migrate long distances and have to decide when to return to their breeding site to reproduce; with varying climate, the normal (i.e. phenological) arrival time could change and birds may breed earlier or later in the season to exploit resources best (Both and Visser 2001; Frederiksen et al. 2004).

Climate Variation

The North Atlantic Oscillation (NAO) is a major source of large-scale inter-annual climatic variation in the atmospheric circulation of the region (Hurrell 1995). In the North Atlantic, the NAO is associated with most variation in winter climate and is correlated with global and regional temperature fluctuations (Hurrell 1995; Hurrell and Van Loon 1997). The NAO index is based on the difference of normalized sea level pressure between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland since 1864. The winter index comprises the months of December through March, including the measure of December of the previous year and January to March of any particular year. During winter, the NAO has a stronger effect on the variability of the climate in Europe, where it can modify

temperature in patterns that last many years (Hurrell 1995). The NAO has positive or negative phases, the changes in pressure gradient from one phase to the other produce large changes in wind speed and direction over the North Atlantic. The heat and moisture transport between the Atlantic and its surroundings varies markedly, seen as winter storms and associated weather (Hurrell et al. 2001). In the past decades, there has been an especially high rate of warming, this increase in average winter temperatures across Europe is accounted for by an increase in the NAO (Hurrell 1995).

Changes in the NAO have a wide range of effects on marine and terrestrial ecosystems, including distribution and population abundance of fish, the flowering dates of plants, and the growth, reproduction, and demography of many land animals (Hurrell et al. 2001). The climate variation associated to the NAO gives the opportunity to assess the effects on breeding performance in wild animal populations (Forchhammer et al. 1998; Przybylo et al. 2000; Sanz 2002). In particular, the increase in spring temperatures (as a result of positive NAO values) has been related to modifications of breeding dates for many species of birds (Crick et al. 1997; Forchhammer 1998; Crick et al. 1999; Przybylo et al. 2000; Sanz 2002). Birds rely on environmental cues to initiate breeding (Frederiksen et al. 2004); in migratory species the changes in temperature may affect their timing making them return earlier/later to their breeding grounds. Consequentially, this has an effect on the laying dates and therefore it is possible to see changes in the time of breeding of certain populations from one season to another (Crick 2004).

Long term studies provide the opportunity to observe how the changes in the physical environment affect the dynamics and breeding parameters of certain populations. In the present chapter, I investigate how hatching date has varied during the past 30 years in the Foula colony and if this variation is related to environmental conditions such as food availability and climate change. Both environmental variables have shown changes through the years so I would expect these variations to have an effect on the breeding

biology of great skuas. Evidently birds would be very sensible to low food abundance, it could be expected minimal reproductive success and no recruitment when food is scarce. Also hatching date could be affected by low food supply, I would expect in years of less food abundance later hatching dates than in years with more food. In terms of climatic conditions, if weather changes it is also possible to expect a shift in hatching dates. In warmer winters it could be possible to find birds arriving to the colony and laying eggs early, however this could be closely linked with how the variation in temperature/climate affects their food source. Furthermore, I examine the variation in hatching date in relation to the survival and recruitment into the population. I would expect individuals with earlier hatching dates to have higher probabilities of survival and recruitment. The results are discussed in the context of variation in the environmental conditions of the region.

2.2 METHODS

For more than 30 years great skua chicks have been ringed in large numbers in Foula, Shetland under the BTO scheme. In most years some 30-80% of chicks in the colony have been ringed and measured. As a result of that, there is an extensive data base which includes information such as ringing date, location within the colony, weight and wing length of the chicks. During these years (1975-present) adult birds have been re-trapped using different methods, such as walk-in and spring traps, either as breeders in their territories or nests or as non-breeders attending club sites. Data collected for various other studies of adult birds have been compiled into a data base which contains information such as status and body measures of the birds.

To obtain hatch date I used a logistic growth curve for great skua chicks (Phillips et al. 1997) which derives the age of the individual from its wing length, and then the age in days was deducted from the date they were found, to obtain the hatching date as Julian date (January 1= 1). An

average hatch date per year was calculated to obtain a mean value which includes all the chicks measured in a particular year; this was used as the variable "hatch date". Data of mean hatch date was available from 1975 to 2003 (29 years), however information of status (i.e. survival) of ringed birds is not as consistent, therefore only 26 years were included in the analysis (see 2.3.3). This mean may differ slightly from the mean hatch date calculated from studies of egg laying in marked nests, since only those eggs that hatch successfully produce chicks that can be ringed and measured. However, in most years the hatching success of great skuas is high and consistent, even if overall breeding success is low, so that any bias in estimating hatching dates is likely to be small.

2.2.1 Environmental variables

A number of environmental variables were related to the mean hatching date in order to determine the factors affecting timing of breeding (Table 1). Food availability was assessed with two different variables, one was the Total Sandeel stock Biomass (TSB) in Shetland in tonnes per year and the other one was the amount of combined discards of haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) in the region (ICES 2007, www.ices.dk). Sandeel data (TSB) was obtained from a research survey data in the form of numbers of sandeels in each age class, this was converted to a calculated total stock biomass for each year using the average masses of the different age classes (Davies 2005). The survey data was combined with a relative abundance index and corrected for different survey methods by Davis (2005). Discard quantities are estimated from all demersal stocks, haddock and whiting make the majority of the content from all the combined species. This correlates with contents obtained by otolith analysis of the great skua diet (Votier et al. 2001, 2004c). These two variables (TSB and Discard) were transformed into logarithms to meet the assumption of normality of the analyses.

Breeding success (measured as the number of chicks fledged per nesting pair, using standard methods developed by The Seabird Group) has been recorded annually at the Foula colony. I used these estimates to investigate the relationship between hatching date and breeding success.

Colony size has also been compiled in different surveys at several Great Skua breeding areas in Shetland (Furness and Ratcliffe 2004). Numbers in Foula have been recorded as apparently occupied territories (AOT) which gives a very good estimate of the number of breeding pairs in the colony (Furness 1987; Furness and Ratcliffe 2004). I made linear interpolations between censuses to estimate the number of AOT each year and used that as a measure of colony size (for actual census data see Table 2.1).

The North Atlantic Oscillation (NAO) is the dominant mode of winter climate variability in the North Atlantic region. The corresponding index varies from year to year but also exhibits a tendency to remain in one phase for intervals lasting several years. I used the NAO winter index (Hurrell 1995) to account for the effect of climate change and its relation with hatching date (http://www.cgd.ucar.edu/cas/jhurrell/indices.html).

2.2.2 Recoveries

In order to assess whether the number of birds born in a particular year and that died in the next two years was related to environmental variables, I analysed the great skua ring recoveries files. From the Ringing Recoveries files provided by the British Trust for Ornithology (BTO), I tracked the ring numbers in the Foula database, which includes all the chicks ringed on Foula a particular year (I used data from 1975 to 2003) and their body measurements. I then selected birds that were recovered the year they were born and two years after that. I assumed that all birds hatched approximately in the month of July, and so the analysis of mortality of young birds includes individuals aged up to 29 months (c.900 days). To account for the differences in numbers of chick ringing per year, a proportion was calculated; the number of young recovered birds was

divided by the total number of chicks ringed in that hatching cohort. This proportion was then regressed with yearly variables, such as mean hatching date, breeding success, TSB and Discards numbers and the NAO winter index of the year the recovered birds were born.

To analyse the relationship between environmental variables and hatch date I used linear regressions. I used t-tests to look at differences in hatching date between birds that returned to the colony and birds which fate is unknown; also when analysing mean hatch date of the colony and hatching date of recovered birds. Data were checked for normal distribution, and non-parametric tests were performed when required. All statistical analyses were performed using SPSS 12 (Dytham 2003).

2.3 RESULTS

2.3.1 Environmental variables and hatching date

Hatch date varied widely amongst years, but this variation did not show a significant trend with year (R^2=0.034, p=0.33, N=29 years; Figure 2.1).

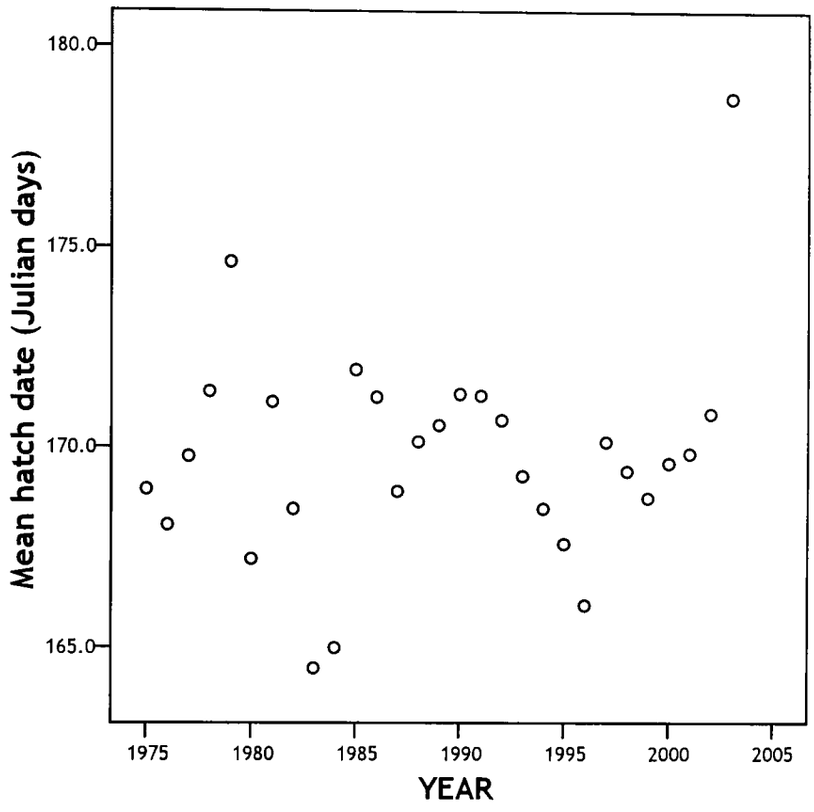


Figure 2.1: Variation of the mean hatch date per year, hatch date is expressed in Julian days with the 1st of January being day 1.

I also found that there was no relationship between mean hatch date and colony size ($R^2<0.001$, $p=0.94$, $N=11$ actual census data only), nor with the NAO winter index ($R^2=0.026$, $p=0.40$; Figure 2.2).

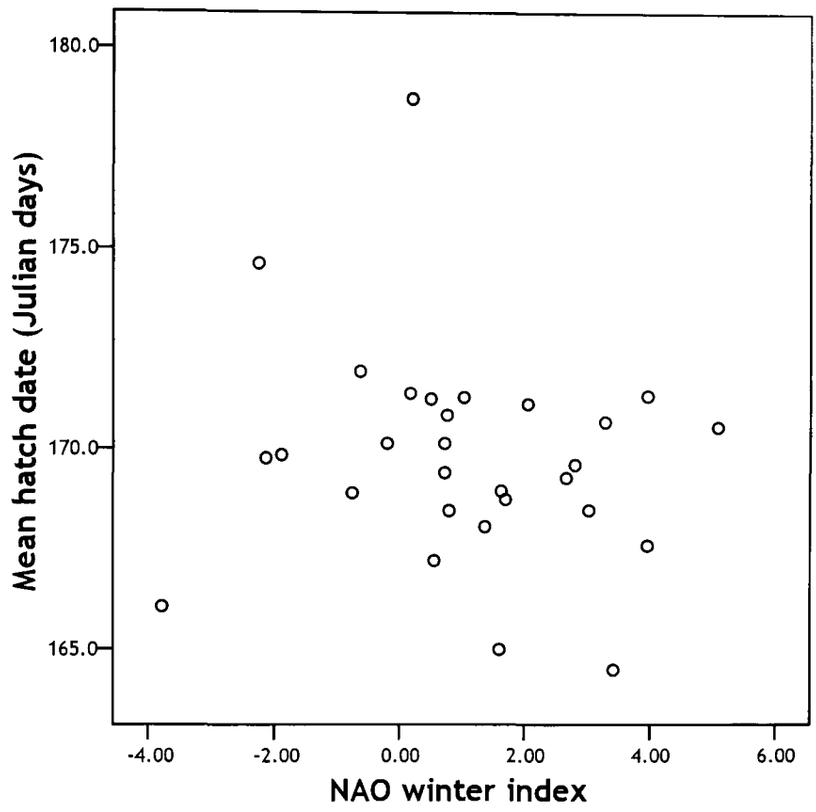


Figure 2.2: Annual variation of the North Atlantic Oscillation Winter Index in relation to the hatch date mean of the Foula colony.

However, TSB was related to the mean hatching date per year (R^2=0.165, p=0.03, Figure 2.3); but not discard (R^2=0.102, p=0.09, Figure 2.4). Hatching was later in years when sandeel biomass or discard quantity was low, though only the former relationship was statistically significant.

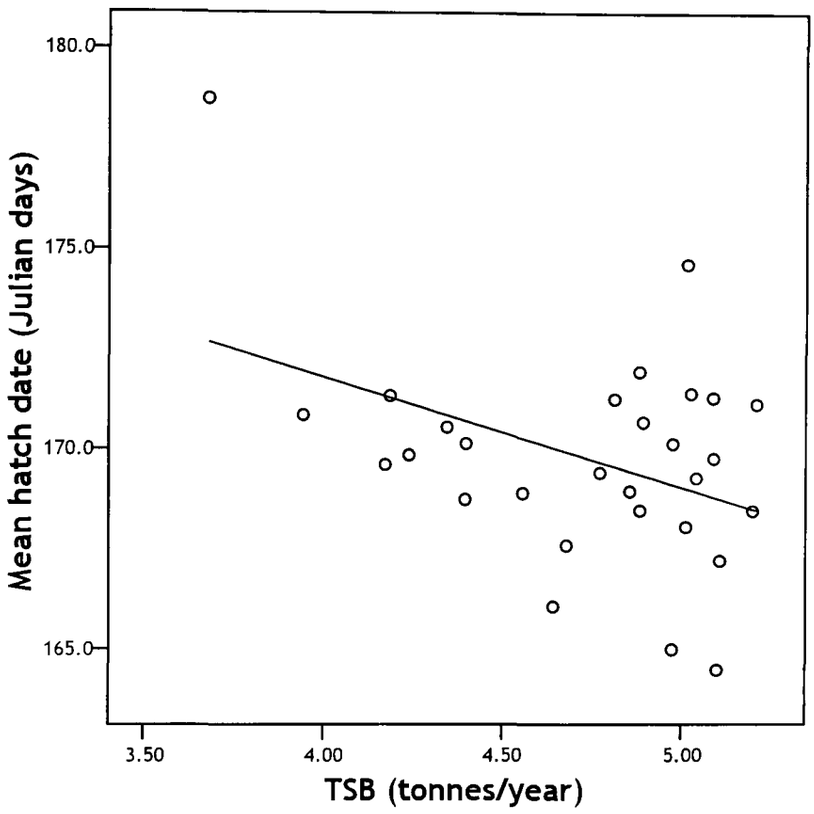


Figure 2.3: Total Sandeel Stock Biomass (logarithm) in the Shetland region, in relation to the mean hatch date per year of the Foula colony.

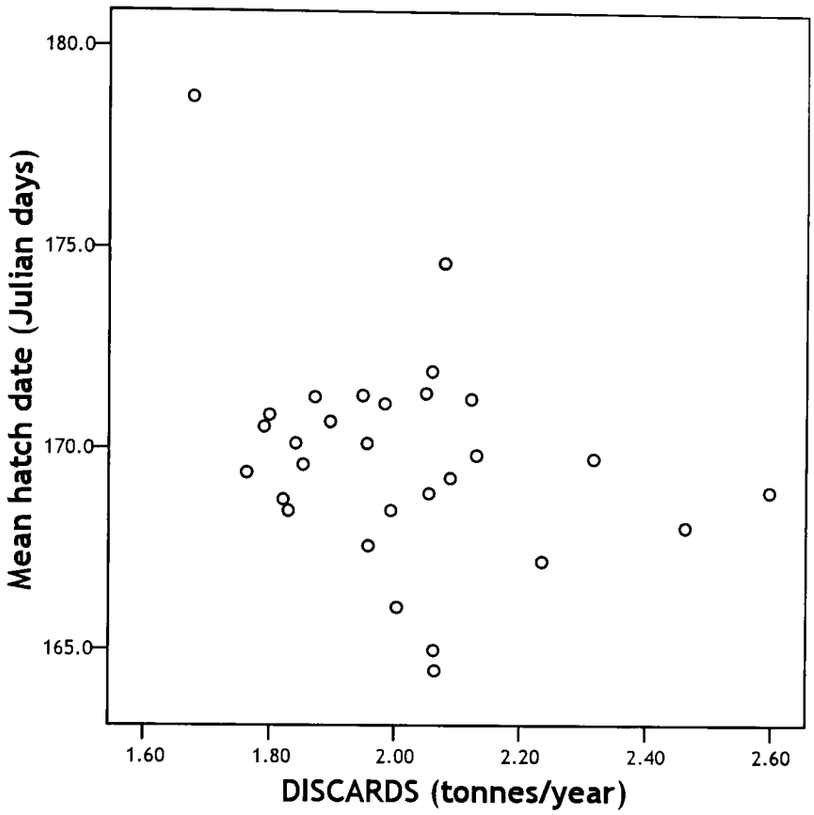


Figure 2.4: Combined measure of discards of haddock and whiting in the Shetland region in relation to the mean hatch date of the Foula colony per year.

Also, the mean hatch date in the colony may explain variation in breeding success. The number of chicks hatched per year was negatively related to the mean hatch date; earlier mean hatching date correlated with higher breeding success in the same year (R^2=0.230, $p<0.01$, Figure 2.5).

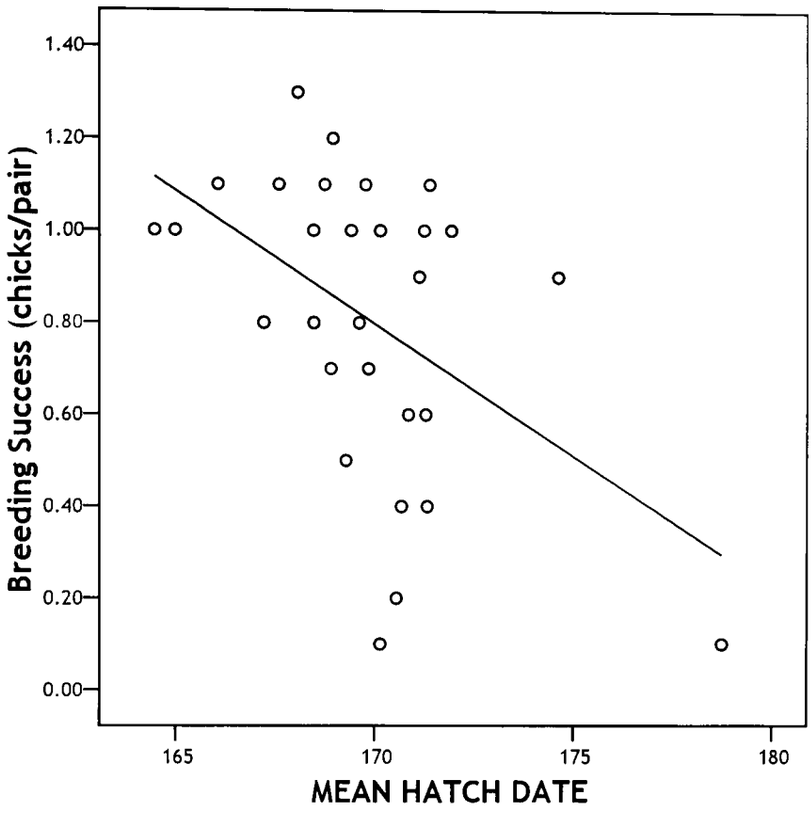


Figure 2.5: Breeding success of Great Skua pairs in the Foula colony and mean hatching date per year (Julian days).

2.3.2 Annual variation of environmental variables

In recent years, the Foula colony has had a lower breeding success than in previous years; breeding success is negatively correlated with year (R^2=0.162, p=0.03; Figure 2.6).

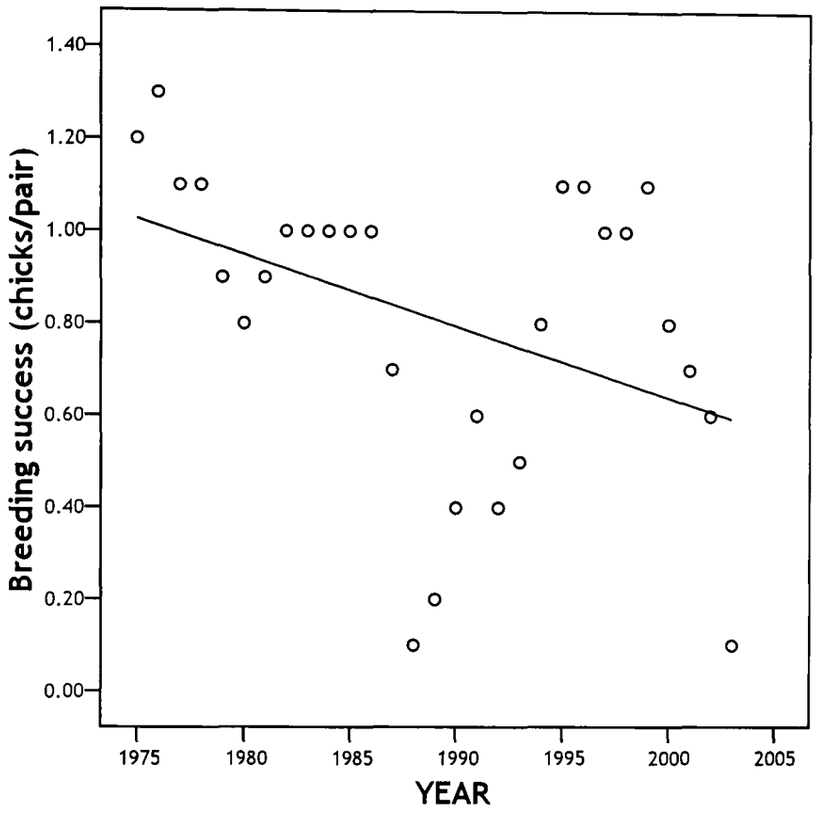


Figure 2.6: Annual variation of breeding success rates in the Foula colony, measured as the number of chicks fledged per nest attempt.

Also colony size has decreased with time, the numbers of AOTs registered are significantly less in recent years than 30 years ago (R^2=0.802, $p<0.01$, N=12 actual census data only; Figure 2.7).

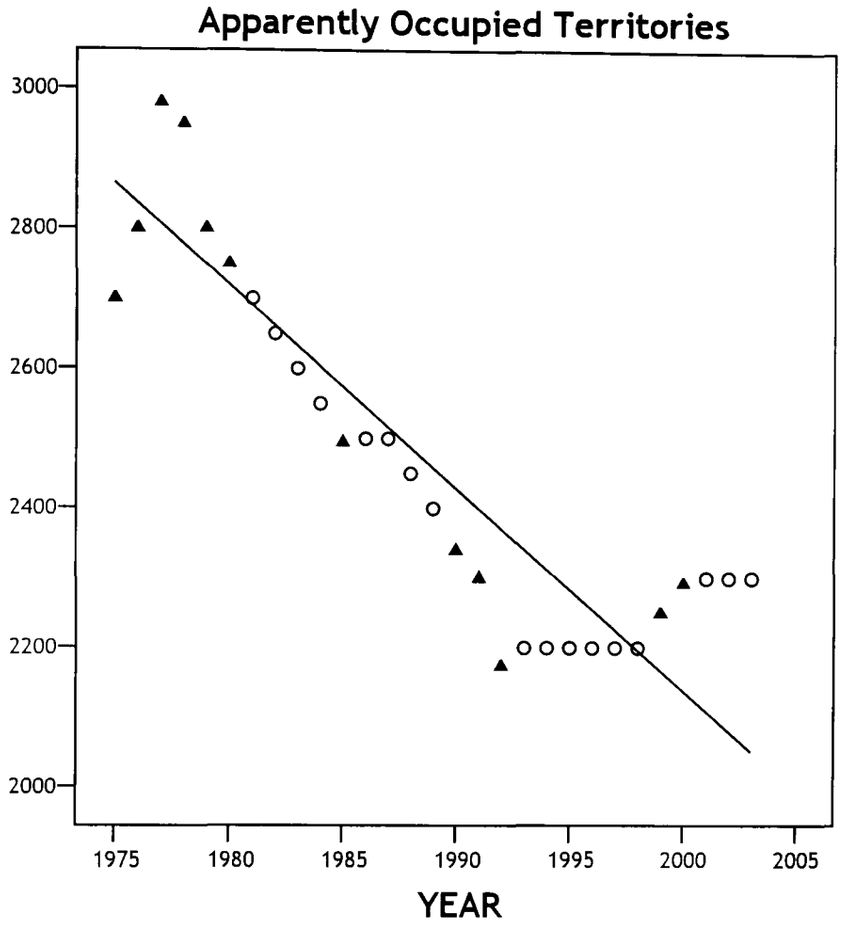


Figure 2.7: Number of Apparently Occupied Territories of Great Skua breeders in the Foula colony between 1975 and 2003 (△= actual census data, N=12; ○= interpolated data, N=17; see Table 2.1).

Although the NAO winter index does not show a significant linear pattern with year (R^2=0.005, p=0.72; Figure 2.8), food availability has varied widely among years, showing a significant negative trend with year in both variables measured (TSB: R^2=0.476, p<0.01; Discards: R^2=0.502, p<0.01; Figure 2.9).

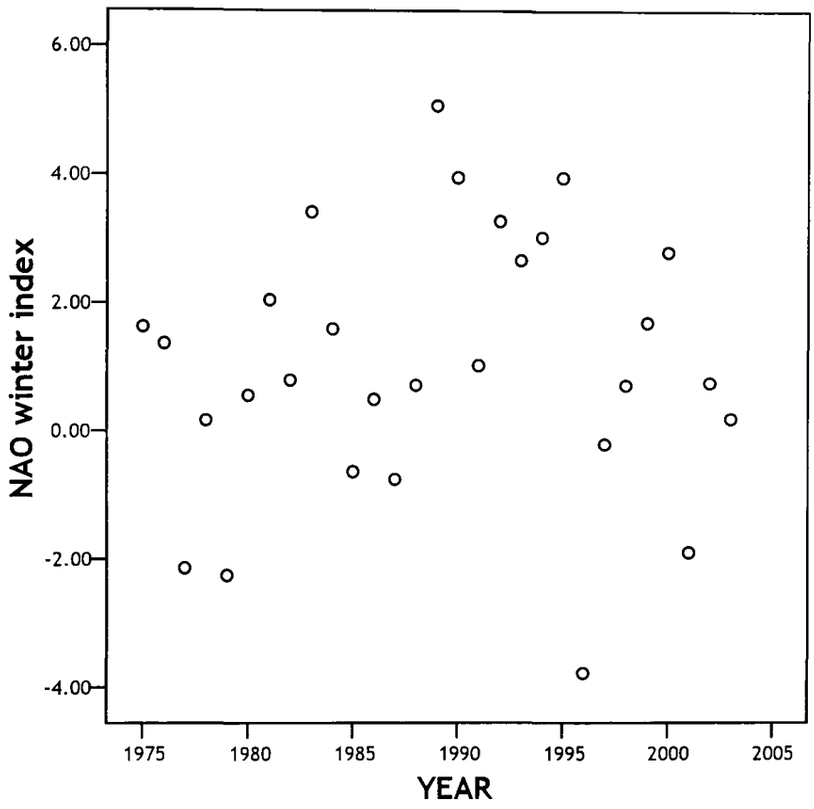


Figure 2.8: Yearly variation of the North Atlantic Oscillation Winter Index (R^2=0.005, p=0.72).

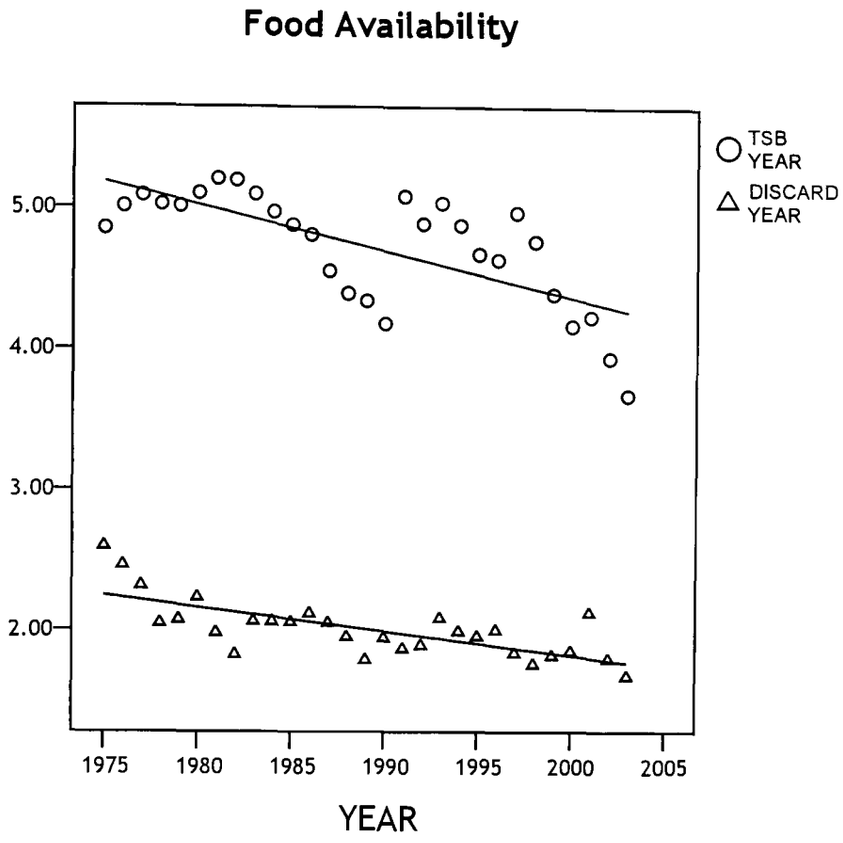


Figure 2.9: Annual variation of food availability in Shetland (○=TSB, △=Discard).

Although the NAO winter index does not relate to the breeding success (R^2=0.078, p=0.143), food availability has a significant positive relationship with breeding success, when sandeels and discards are more abundant the breeding success is higher (TSB: R^2=0.309, p<0.01; Figure 2.10, Discard: R^2=0.247, p<0.01; Figure 2.11)

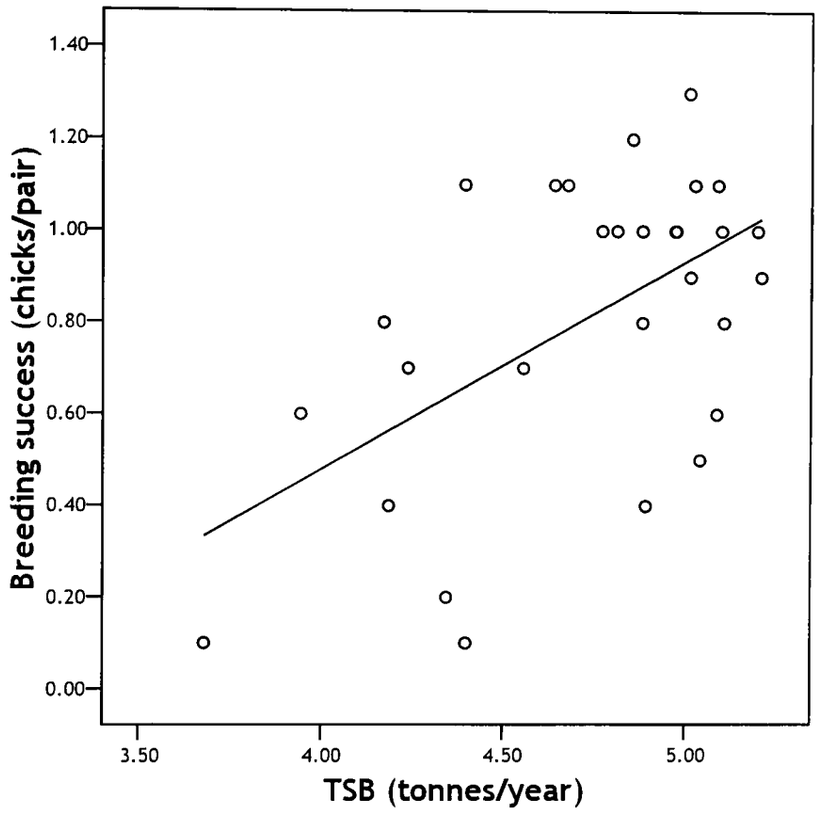


Figure 2.10: Breeding success in the Foula colony measured as chicks per nesting pair since 1975 in relation to total sandeel biomass in Shetland measured in tonnes per year.

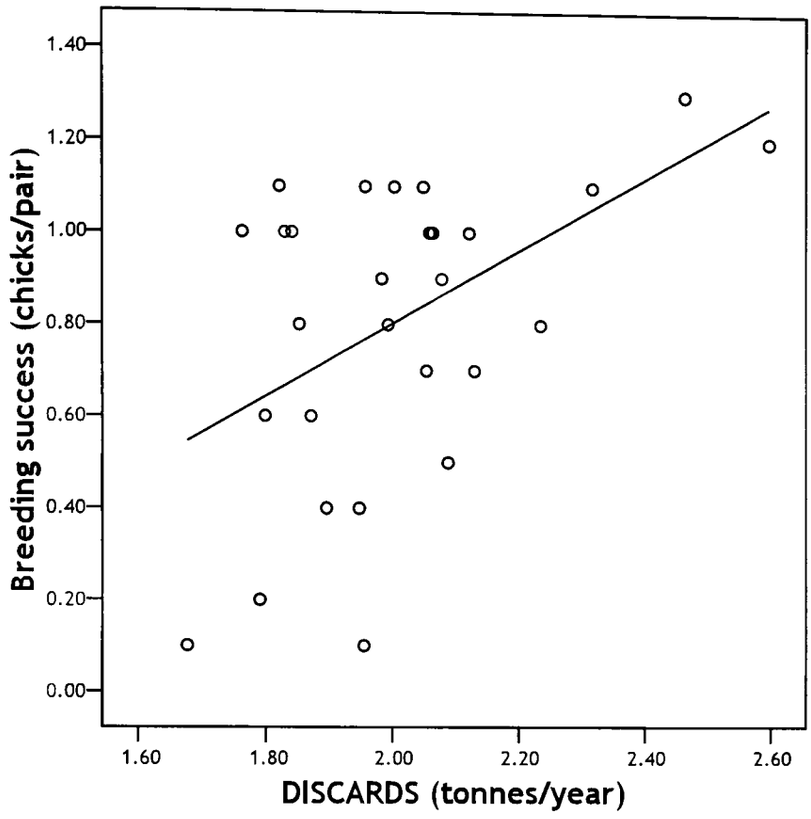


Figure 2.11: Breeding success in the Foula colony measured as chicks per nesting pair from 1975-2003 in relation to combined fishing discards of haddock and whiting in the region measured in tonnes per year.

2.3.3 Return to the colony

When analysed within cohorts, ringed birds that returned to the colony (including birds re-trapped in clubs and birds recruited as breeders) had on average earlier hatching dates than birds of unknown fate (never re-trapped after ringed as chicks) (Paired $t=5.24$, d.f. 25, $p<0.01$, N= 26 years; Figure 2.12, Table 2.2). This yearly difference (measured in days) of the hatch date between recruited and not recruited birds was not related to food availability (TSB: $R^2=0.005$, $p=0.73$; Discard: $R^2=0.001$, $p=0.86$), nor to population size ($R^2=0.024$, $p=0.45$) or climate conditions (NAO: $R^2=0.060$, $p=0.22$). However, there is a positive relationship between breeding success and the difference in hatch date between recruited and not recruited birds, the bigger the difference in each individual cohort the lower the breeding success ($R^2=0.169$, $p=0.04$, Figure 2.13).

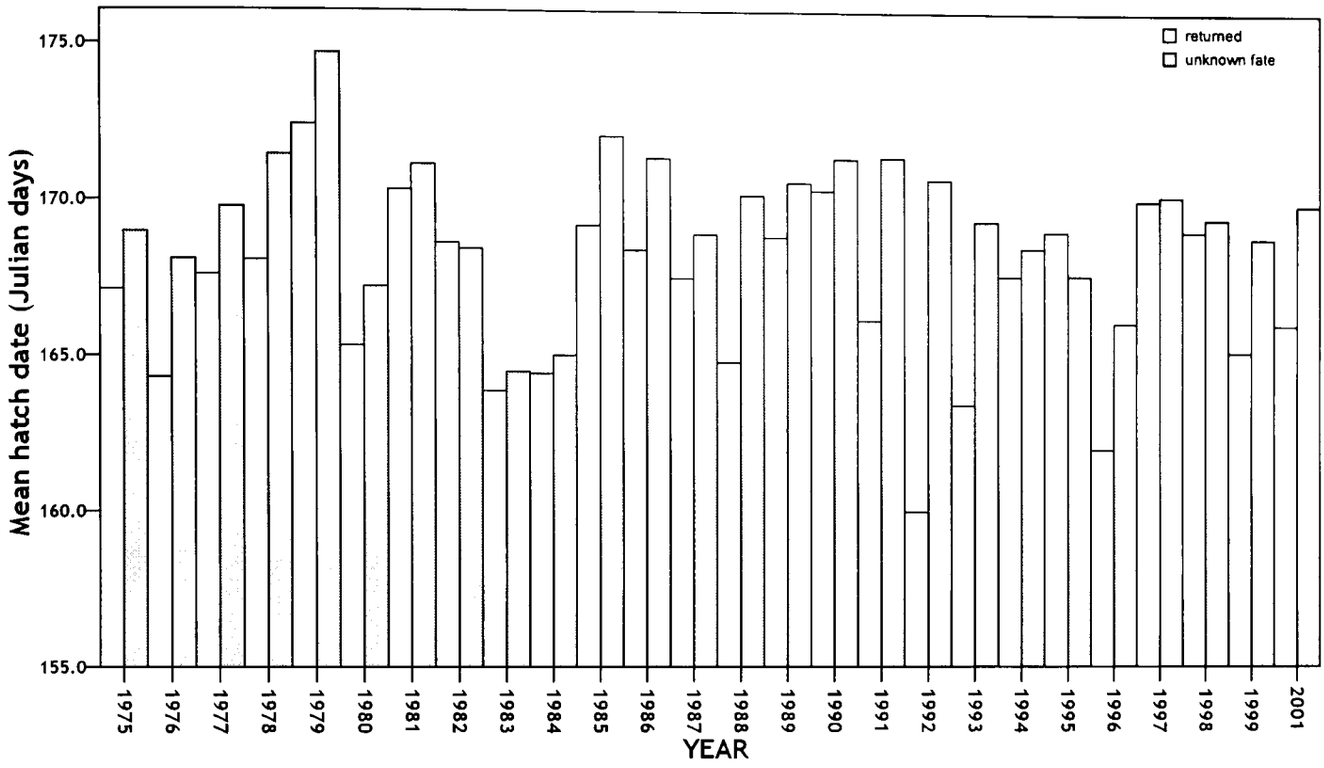


Figure 2.12: Average hatch date (in Julian days, Jan 1st= 1) per year of birds that returned (breeders or club attending birds) to the colony and birds which fate is unknown. Average hatch date for returned= 166.9 and for unknown fate= 169.4; N=26 years. Missing years have no records of ringed birds.

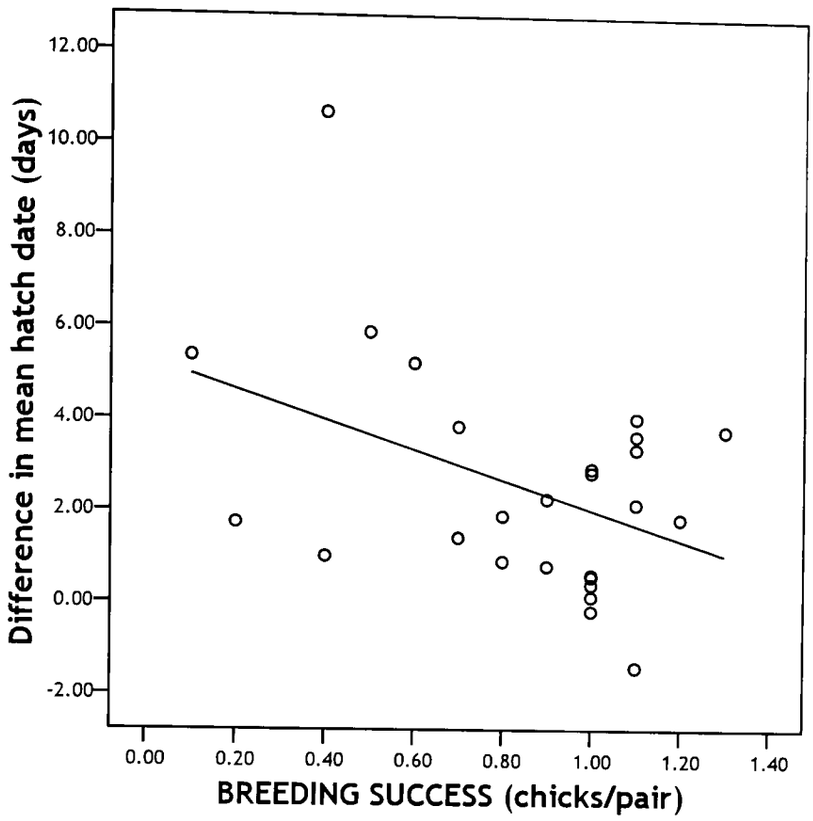


Figure 2.13: Difference in hatch date (in days) between birds that returned to the colony and birds of unknown fate in relation to annual breeding success in the Foula colony.

2.3.4. Recoveries

The mean hatching date of young birds (up to 900 days old) recovered per cohort is not significantly different to the mean hatching date of the colony for that year ($t=-1.56$, $p=0.13$, $N=29$ years). There is no linear relationship between the proportion of young birds recovered and year they were born ($R^2=0.006$, $p=0.69$, $N=29$ years; Figure 2.14). The mortality of young individuals during the two consecutive cohorts after they were born, is not related to the mean annual hatch date or to the breeding success of the colony in the year they were born (Hatch date mean $R^2=0.082$, $p=0.13$; Breeding success $R^2<0.001$, $p=0.95$). Also, environmental variables analysed did not seem to have an effect on the mortality of young birds, neither food availability nor the NAO winter index had a relationship with the

proportion of young birds recovered out of the chicks ringed in a particular year (NAO: R^2=0.006, p=0.69; TSB: R^2=0.009, p=0.62; Discards: R^2=0.003, p=0.77).

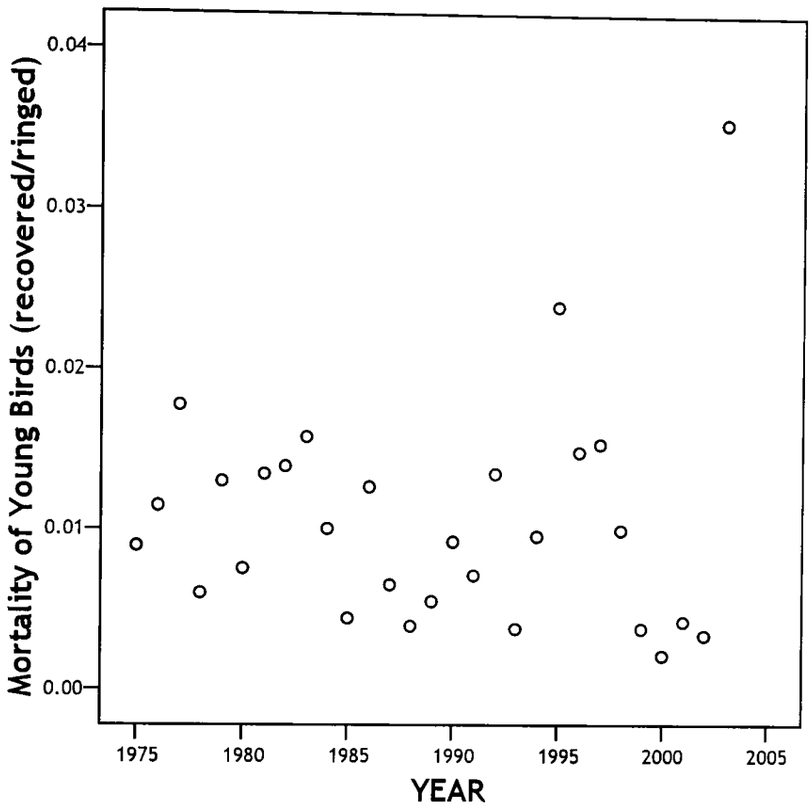


Figure 2.14: Proportion of birds aged up to 29 months recovered, in relation to number of chicks ringed in Foula in a particular year from 1975 to 2003.

2.4 DISCUSSION

2.4.1. Environmental variables and hatching date

The average hatching date of Great Skuas in the Foula colony has varied for the last 30 years (range of 14 days); this variation does not seem to be systematic, but only becoming earlier or later in particular years. However, it is important to give a closer look at the variation in each specific year and relate that to the environmental conditions that may be affecting the breeding parameters of the colony. Since 1990, the mean hatching date

decreased for a period of 6 years (range of 5 days), after that period the colony registered an increase in the mean hatching date. Overall, the variation in hatching date was not significantly correlated to colony size, but if we look at the number of breeding pairs during that period we could see numbers falling. It has been suggested before that a decrease in the number in breeding pairs would signify early hatching days if this reflected a lack of recruitment and so there were fewer inexperienced pairs (which tend to lay late) (Furness 1987), so in particular years hatching date could be associated to colony size. On the other hand, colony size did not prove to have a significant effect on hatching date during the 30 years of data analysed in this study. Breeding pairs in Foula are not constrained by space, and it is likely that the variation in hatching date is related to other environmental factors.

Great skuas are top predators in the marine food web, their diet is rather varied, exploiting a wide range of food sources: fishery discards, sandeels, and other seabirds (Phillips et al. 1997; Votier et al. 2001, 2003). There is a close relationship between fisheries activity and their feeding choices, as well as the numbers in the colony (Votier et al. 2004a, 2004c). Although the main composition of their diet (more than half of the total) in Shetland is sandeel (Furness and Tasker 2000), they also depend on fisheries discards and when this source is scarce they become predators of other seabirds (Votier et al. 2004a, 2004b). Exploiting a different source of food can mean a change in the breeding outcome (Gill et al. 2002). Skuas that predate on other seabirds have earlier hatching dates and thus better breeding performance (Votier et al. 2004a). Breeding success is correlated to food availability and diet composition; in years where sandeel stock and fisheries' discards are abundant, there is a higher production of fledglings per nest. Breeding success is also correlated to hatching date, in those years when chicks hatch earlier the breeding success is higher than in years with later hatching dates. It is possible that in those years fledglings have more opportunities to survive and may be in better body condition. Hatching date has a statistically significant negative relation with sandeel

abundance, but this is not the case for the other food variable measured: discard abundance. In these two analyses it is notorious the data point for hatching date in 2003; this was the latest in the season it has been registered since 1975. From personal observations and other unpublished data from monitoring the colony (R. Furness pers. comm.) I gathered that the conditions for the colony in terms of food abundance and the outcome of reproduction in the next two seasons (2004-2005) was similarly or equally poor, therefore I would predict that including the following seasons would give statistical strength to the analysis. Sandeel comprises the majority of the diet and birds are more sensitive to any variation in the supply of sandeel than of any other component of their diet. It is possible that in years when sandeel stock is low parents delay reproduction and hatch later in the season, when food is more abundant and they would not compromise their own survival. This in turn could have consequences for the survival of the young as later in the season food may become scarce and competition may be severe.

Although it would be expected from other studies to find a relationship between the weather conditions and hatching date, the NAO winter index did not directly explain the variation in the mean hatching date per year. Over the past decade the values of the NAO winter index have been mainly positive, which implies warmer weather (Hurrell 1995), and it has been suggested that climate change could affect all elements in the food chain (Thompson and Ollason 2001; Crick 2004); therefore the effect of changing climate conditions over long periods of time on the variation of mean hatching date could be indirect, and operate through the food chain. Recent examples show that birds are shifting their laying dates over long periods of time in relation to changing climatic conditions (McCleery and Perrins 1998; Brown et al. 1999; examples in tree swallows (*Tachycineta bicolor*): Dunn and Winkler 1999; collared flycatchers (*Ficedula albicollis*): Przybylo et al. 2000; and blue tits (*Parus caeruleus*): Sanz 2002; effects on recruitment: common guillemots (*Uria aalge*): Crespin et al. 2006). This could suggest that the effect is mainly produced by changes in food availability. Great skuas depend on fish, but further down the food chain,

plankton is affected by warmer temperatures therefore an indirect effect of warmer weather could be affecting the food supply at the beginning of the breeding season. Changing climate conditions and human interactions could affect the food availability and this in turn could have an effect on the breeding parameters of seabirds, in particular great skuas, which are a fairly sensitive species (Furness and Tasker 2000). The consequences of low sandeel abundance could be reflected in a decline of the Great Skua breeding success in the long term, although their ability to exploit other sources of food could buffer this situation in the mean time.

2.4.2 Survival, recruitment and hatching date

Hatching date can affect post-fledging survival and recruitment (Prevot-Julliard et al. 2001; Reed et al. 2003). Hatching earlier in the season brings advantages in terms of better access to resources (i.e. food availability), resulting in better body condition in the first stages of their lives. Also, late-hatched birds are less able to compete for breeding sites, and could end up nesting in less desirable spaces (Prevot-Julliard et al. 2001). Environmental conditions play an important role in survival to recruitment age, extreme or changing weather could represent a reduction in food availability, challenging unfit and inexperienced birds attempting to breed (Reed et al. 2003). Over 30 years of data in the Foula colony, I found that birds returning to the colony (either as breeders or attending club-sites) had earlier hatching dates than birds of unknown fate (defined here as "not recruited"). The difference in days (range up to 5 days) between the hatching days of "recruited" and "not-recruited" birds was not related to environmental variables (food availability, NAO) or colony size. However, the difference in hatching date between "recruited" and "not recruited" birds was significantly greater in years with low breeding success, early hatched birds returned to the colony whereas late hatched individuals did not survive or emigrated. In years of low breeding success early-hatched birds were at an advantage and had higher probability of returning to the colony (Figure 2.13). It is well known that hatching early is advantageous in

the early stages of life, often related to chick survival and growth in different bird species (e.g. Cooch et al. 1991; Sydeman et al. 1991; Burger et al. 1996; Arnold et al. 2004; and in great skuas: Catry et al. 1998). Therefore, in highly competitive situations early-hatched birds succeed relatively better than late chicks in returning back to their natal colony and in turn find a nesting space to breed.

The effects of breeding parameters such as hatching date and parental care could be stronger during the early life stages of an individual (Spear and Nur 1994; Catry et al. 1998). Hence, it would be expected to find a relationship between mortality and hatching date, but after analysing ring recovery data of the past 30 years the results show no effect of mean hatching date and the proportion of 1 and 2 year old Great Skuas recovered. This was also the case for the other environmental variables measured, there was no significant relationship between mortality of 1 and 2 year old birds and food availability at Shetland, or changing weather conditions (NAO winter index). The large number of great skua chicks ringed every year contrasts with the small number of rings recovered by the BTO. This is likely to be expected due to the fact that the majority of birds die at sea and recovery of rings is impossible. Thus, sample size is reduced and statistical analyses prove to be less powerful.

Since 1975 there has been variation in the conditions around the Foula colony; food has become less abundant (both sandeel stock and discard numbers have decreased) which is associated to a decline in breeding success over the same period and a decline in the number of breeding pairs. Climate conditions have also changed impacting the whole ecosystem and probably indirectly affected great skua breeding success. The repercussions of these changes are becoming more evident in later years and it is expected to continue as the colony reaches its carrying capacity (Furness and Ratcliffe 2004). Young birds in better body condition would have a better chance to return to recruit in their natal colony whilst their counterparts could face the decision of emigration (see Chapter 5). To complement the results obtained from this study, other colonies could be examined to see the effects of environmental variables on hatching date

and breeding success, as well as on the recruitment rate. Colonies are subject to different "pressures" depending on size and density, Foula is the biggest colony of great skuas so events occurring here may be different from smaller colonies or colonies with different densities.

Whilst for this study there was a good long term sample of hatching dates and there is a high recovery of ringed birds (as breeders or as non-breeders), some information is still lacking. The relationship between hatching date and recruitment could be an effect of parental quality, therefore birds that hatch early from higher quality parents would be in an advantage to return to the colony and breed. It would be ideal to be able to separate between parental quality and the environmental variables of a particular cohort (which could also affect hatching date), by an experimental design in which parental quality is teased apart and manipulated with respect to hatching date (Blomqvist et al. 1997; Wendeln and Becker 1999). It would also be interesting to find out whether individuals hatched early in the season, return to the colony in better body condition than later hatched birds or if early hatching is reflected in any other individual trait related to recruitment. Unfortunately this was not possible to analyse in this study, because not all birds for which body condition is known had been ringed as chicks (and have a known hatching date).

Table 2.1: Number of chicks ringed per year in Foula and environmental variables measured.

YEAR	No. chicks ringed	Mean hatch date (Julian days)	S.D. (days)	Breeding success (chicks/ pair)	TSB (tonnes)	DISCARDS (000 tonnes)	Colony size (AOT)
1975	1834	168.95	7.47	1.2	71759	395.4	2700*
1976	2052	168.06	8.63	1.3	102834	290.3	2800*
1977	2585	169.77	6.49	1.1	123122	207.3	2980*
1978	997	171.39	5.90	1.1	106344	111.9	2950*
1979	1537	174.63	6.97	0.9	103595	119.7	2800*
1980	1943	167.21	6.26	0.8	128095	171.7	2750*
1981	1125	171.13	6.48	0.9	162087	96.1	2700
1982	788	168.46	5.16	1	158267	67.5	2650
1983	1330	164.48	5.79	1	126071	115.9	2600
1984	990	164.99	5.29	1	93994	115.4	2550
1985	1116	171.94	6.50	1	76377	114.4	2495*
1986	1025	171.25	6.02	1	65097	132.2	2500
1987	737	168.90	5.60	0.7	36047	113.2	2500
1988	746	170.14	7.36	0.1	25041	90.1	2450
1989	323	170.55	7.08	0.2	22145	61.7	2400
1990	304	171.33	5.63	0.4	15341	88.6	2340*
1991	280	171.29	7.12	0.6	122635	74.3	2300*
1992	222	170.68	6.78	0.4	78152	78.6	2174*
1993	779	169.28	7.23	0.5	110108	122.5	2200
1994	415	168.47	6.19	0.8	76515	98.4	2200
1995	250	167.59	4.69	1.1	47706	90.6	2200
1996	470	166.06	4.96	1.1	43867	100.7	2200
1997	650	170.14	6.51	1	94589	69.3	2200
1998	400	169.41	5.97	1	59221	57.9	2200
1999	524	168.74	5.99	1.1	24895	66.2	2250*
2000	467	169.61	5.85	0.8	14860	71.2	2293*
2001	467	169.85	5.24	0.7	17330	134.8	2300
2002	585	170.85	5.86	0.6	8771	69.2	2300
2003	169	178.74	6.12	0.1	4769	47.5	2300
2004				0.01	3255	30.0	
2005				0.3			

*actual census data

Table 2.2: Annual hatch date mean (in days) of birds "recruited" to the Foula colony and birds which fate is unknown. T-tests were performed for each individual year, for non-parametric data Mann-Whitney tests are reported. Also shown is the difference in days of not recruited birds hatch date mean from recruited birds hatch date mean.

YEAR	Recruited	N=	Not recruited	N=	t/U=	p=	Difference (days)
1975	167.12	16	168.97	1818	-0.98	0.32	+1.85
1976	164.31	29	168.10	2023	-2.35	**0.02**	+3.79
1977	167.61	18	169.78	2567	-1.41	0.15	+2.17
1978	168.06	16	171.44	981	-2.28	**0.02**	+3.38
1979	172.41	41	174.69	1496	-2.06	**0.04**	+2.28
1980	165.33	33	167.23	1912	-1.73	0.08	+1.9
1981	170.33	33	171.14	1091	16575	0.43	+0.81
1982	168.62	29	168.45	759	0.17	0.86	-0.17
1983	163.88	45	164.50	1285	-0.69	0.48	+0.62
1984	164.44	52	165.02	938	-0.76	0.44	+0.58
1985	169.19	47	172.05	1069	-2.96	**0.003**	+2.86
1986	168.40	37	171.35	988	13444	**0.006**	+2.95
1987	167.50	16	168.92	721	-1.007	0.31	+1.42
1988	164.80	5	170.17	741	994.5	0.07	+5.37
1989	168.83	6	170.58	317	850	0.65	+1.75
1990	170.33	6	171.34	298	-0.43	0.66	+1.01
1991	166.16	6	171.39	274	-1.78	0.07	+5.23
1992	160.00	1	170.68	*222	n/a	n/a	+10.68
1993	163.44	9	169.34	770	1649	**0.007**	+5.9
1994	167.57	7	168.48	408	-0.38	0.7	+0.91
1995	169.00	1	167.59	*250	n/a	n/a	-1.41
1996	162.00	1	166.06	*470	n/a	n/a	+4.06
1997	170.00	2	170.14	*650	n/a	n/a	+0.14
1998	169.00	3	169.41	*400	n/a	n/a	+0.41
1999	165.12	8	168.79	516	-1.72	0.08	+3.67
2001	166.00	1	169.85	*467	n/a	n/a	+3.85

* year mean was used

n/a = Not-available data because "recruited" sample was too small.

There was no data available for 2000, 2002-03 (no ringed birds were found for those years).

3. Differences in body condition between breeders and non-breeders, a long term study

3.1 INTRODUCTION

Seabirds generally spend a few years visiting colonies before breeding for the first time, this period of time is thought to be so they can achieve maturity and the desirable skills in order to reproduce (Furness and Monaghan 1987). Recruitment is affected by several factors and one of them is the body condition of the potential recruits (Porter and Coulson 1987; Both et al. 1999). Age of first breeding could vary according to differences in body condition of the birds, as well as to other physiological and social factors. Porter and Coulson (1987) demonstrated that recruits were heavier than prospectors, implying that larger size (i.e. body weight) is a prerequisite for recruitment (Porter and Coulson 1987). The difference in body size of pre-breeders suggests that there is considerable competition at the time of recruitment, and that larger individuals are at an advantage compared to smaller birds in acquiring a territory for breeding (Porter and Coulson 1987). Later, Porter (1988) suggested that the difference in individual quality might cause the variation in the recruitment rates of a colony, and that an individual selection occurs at the time of recruitment (Porter 1988). In breeding colonies there are often sites that are more densely populated and that appear to be more desirable to breeders and to prospectors. There is high competition for these areas and they are very aggressively defended by territory holders. Therefore, new recruits are better quality individuals which are able to face aggression and sustain a territory; it is also possible to expect that less quality birds would take spaces in less desirable spaces often at the edge of the colonies or will not breed at all (Porter 1990).

Individual body condition and body reserves influence reproductive success, therefore birds in better body condition are more likely to attempt breeding (e.g. Chastel et al. 1995; Barbraud and Chastel 1999). If in order to gain a territory in a competitive colony or site prospecting birds have to achieve a certain level of body condition, then it could be expected that non-breeders (without a territory) would be in poorer condition than breeding birds (holding a territory). Environmental conditions have changed

during the past decades; changes in food abundance, climate and density are thought to affect breeding success and recruitment rates in a population (Chapter 2) and it is possible that they could affect the body condition of birds. The present chapter assesses the differences in body size and condition between prospectors and established breeders in the Foula colony, by analysing recently collected and long-term data (30 years) of body condition. I expect to find differences in size and body condition between non-breeders and breeders; however these might be influenced by environmental conditions such as food availability, and competition within this particular population. Because the three parameters recorded (see below) reflect different aspects of individual body condition, it is possible that the results of the three measures will not concur, however the measures of body size give a more direct comparison. If non-breeders are of less quality (smaller in size or in poorer body condition) than breeders, then it is possible to assume that they need to reach a certain level of "condition" to acquire a territory in this particular colony.

Measuring Body Condition:

Body Mass Index (BMI)

The body mass index is a widely used measure of body condition in field biology and especially in birds. This index shows mainly the lipid reserves in the body (Zwarts et al.1996). I calculated this index from the linear regression between body weight and body size. I used the residuals of this regression as an individual measure of body condition. Body size was represented by the first factor extracted from a Principal Components Analysis (PCA) including the different body measures (see Results).

Mean Corpuscular Volume (MCV)

The mean corpuscular volume is a combined measure of erythrocyte and haematocrit counts and it has been correlated with parameters such as breeding performance in Great Skuas (Bearhop et al. 1999). This blood parameter could give an indication of body condition since it is a direct

measure of red blood cell production. In a healthy bird a small proportion of cells are immature, and these immature erythrocytes are larger. Therefore elevated values of MCV could be related to the effect of stress requiring increased production of red blood cells, whereas reduced MCV may indicate a lack of production of new red blood cells (Bearhop et al. 1999). It is expected that birds in poor condition would have higher values and birds in good condition would have low values.

Pectoral Muscle Volume (PMV)

The pectoral muscle volume can reflect the protein condition of the bird, since it is the largest protein storage and it is an important source of protein during breeding (Jones and Ward 1976; Houston et al. 1995; Bolton et al. 1991). Following Bolton et al. (1991), I took direct measures of the birds' pectoral muscle using a length of soldier wire that was traced across the pectoral area beneath the feathers perpendicular to the sternum. Two profiles were taken for each bird and then sprayed onto paper to leave an outline. From the highest point of the profile, an area of 3cm width was calculated; the average area was later multiplied by the sternum length, thus obtaining the volume of the pectoral muscle (Bolton et al. 1990, area (ii), method E; see Kalmbach et al. 2004).

3.2 METHODS

The study was conducted in Foula, during the breeding seasons of 2003 and 2004 (May to July). Trapping of Great Skuas occurred in two of the major club sites of the colony, and in the surrounding breeding areas. Non-breeding birds were baited and trapped using either a string-controlled net powered by elastic or a camouflaged radio-controlled spring trap. Breeders were caught with the radio controlled traps on their nests. It was only possible to catch a few birds per day, therefore the sample is distributed sporadically across the three months of fieldwork. Laying dates were calculated by direct observation and in some cases by measuring the eggs

or chicks and comparing against egg density in relation to stage of incubation or a logistic chick growth curve (Furness 1986). Non-breeding birds were assigned a unique combination of plastic colour rings and a metal BTO ring when absent. In most of the cases, breeders were previously ringed (metal and colour rings). Several body measures were taken (±0.1mm): tarsus length, total head and bill length, maximum flattened wing-chord, sternum length, and body weight (±10g). Also a profile of the pectoral muscle was taken using solder wire, following the method described by Bolton et al. (1991). Approximately 1ml of blood was collected from the tarsal vein (under Home Office license) and it was separated into two samples, one of them was frozen in an eppendorff plastic tube containing EDTA and then used for sexing birds caught in 2003-04. Sexing was done following the method described by Griffiths et al. (1998) in which two CHD genes are identified and multiplied using PCR techniques; the CHD-Z gene occur in both sexes, but the CHD-W only occurs in females. The other blood sample was collected into a paediatric tube containing KEDTA, and into two heparinised capillaries for heamatocrit analysis and cell counts for MCV (2003 season only, see Kalmbach et al. 2004). The MCV is a combination of two measures: Packed Cell Volume and Red Blood Cell counts. The PCV is obtained by spinning the capillary tubes and measuring (±0.1mm) the proportion of red blood cells; the RBC count is obtained by direct measurement of stained cells in a Neubauer counting chamber. Both measures are combined in this formula 1000 x (PCV/RCB 10^{12}/l) (Kalmbach et al. 2004).

From data collected in Foula for the past 30 years in breeding territories and in club sites, I analysed two comparable files; one from the 1970s (R.W. Furness) and another from the 1980s (N.I. Klomp and K.C. Hamer).

Statistical analysis was done using SPSS 12. To test for relationships between variables I used Regressions and Analyses of Covariance (including body size as covariate). To test for differences I used T-test; data was tested for normal distribution and non-parametric tests were performed when required.

3.3 RESULTS

In 2003, 103 birds were caught, 42 non-breeders (24 males and 18 females), and 61 breeders (25 males and 36 females), and in 2004, 46 birds were caught, 29 non-breeders (13 males and 16 females) and 17 breeders (5 males and 12 females). There was no differences in the average trapping date between breeders and non-breeders in 2003 ($t=1.19$, $p=0.23$, $d.f.=101$) nor in 2004 ($t=0.78$, $p=0.44$, $d.f.=44$).

Females were larger than males in all the body measures taken, apart from sternum length (Table 3.1). Due to size dimorphism, subsequent analyses were performed separately for females and males.

Table 3.1: Biometrics of birds caught in Foula during 2003 and 2004. Comparison between body measures of males and females.

	Sex	Mean	s.d.	t	p
Weight	male	1301	88	8.83	<0.001
	female	1430	89		
Tarsus	male	80.6	1.8	4.12	<0.001
	female	81.8	1.7		
Head and bill	male	110.8	1.9	3.27	0.001
	female	111.9	1.9		
Wing	male	413.2	8.2	7.96	<0.001
	female	423.8	7.9		
Sternum	male	126.3	11.8	0.35	0.72
	female	127.0	11.7		

3.3.1 Comparison between breeders and non-breeders

Biometrics

In males, there were no significant differences in size between breeders and non-breeders apart from wing length; breeders had larger wings than non-breeders:

Table 3.2: Body measures of Male Breeders and Non-breeders

	Breeders	Non-breeders	t	p
Tarsus	80.8±2.0	80.4±1.6	0.97	0.33
Head and bill	110.5±2.2	111.1±1.6	1.13	0.26
Wing	417.4±7.1	409.7±7.5	4.27	<0.001
Sternum	128.2±12.9	124.9±12.9	1.09	0.27
Weight	1304±104	1297±75	0.32	0.75

In females, breeders had larger sternum and wing measurements but these differences were not significant, however non-breeders were heavier than breeders:

Table 3.3: Body measures of Female Breeders and Non-breeders

	Breeders	Non-breeders	t	p
Tarsus	81.8±1.9	81.9±1.5	0.28	0.78
Head and bill	111.8±2.2	112.0±1.5	0.39	0.69
Wing	425.1±7.4	421.8±8.3	1.87	0.06
Sternum	129.0±10.6	124.2±12.8	1.85	0.06
Weight	1408±87	1460±83	2.67	0.01

Body Condition

Mean Corpuscular Volume was only measured in 2003 and there was no differences in blood cell counts between breeders and non-breeders, males and females were combined for this analysis ($F_{1,57}$=1.11, p=0.29).

There were yearly differences in PMV between breeders and non-breeders, in 2003 breeders had higher values, while in 2004 non-breeders had higher values; however none of these relationships were statistically significant (ANOVA with status as factor, 2003: $F_{1,96}$=2.99, p=0.08; 2004: $F_{1,44}$=3.39, p=0.07).

Four body measures were included in the PCA to obtain one overall measure of size. Body size was the first factor of the PCA that included sternum, head and bill, tarsus and wing length (45.50% of variance explained for males and 41.28% for females). Body mass was regressed over body size and the standardized residuals of this equation were used as the BMI (Males: R^2=0.143, p=0.002, N=64; Females: R^2=0.199, p<0.001, N=80).

Non-breeders had higher values of BMI than breeders (ANCOVA with status as a factor, $F_{1,146}$=6.70, p=0.01, Figure 3.1), the model was not significant for covariates year or body size.

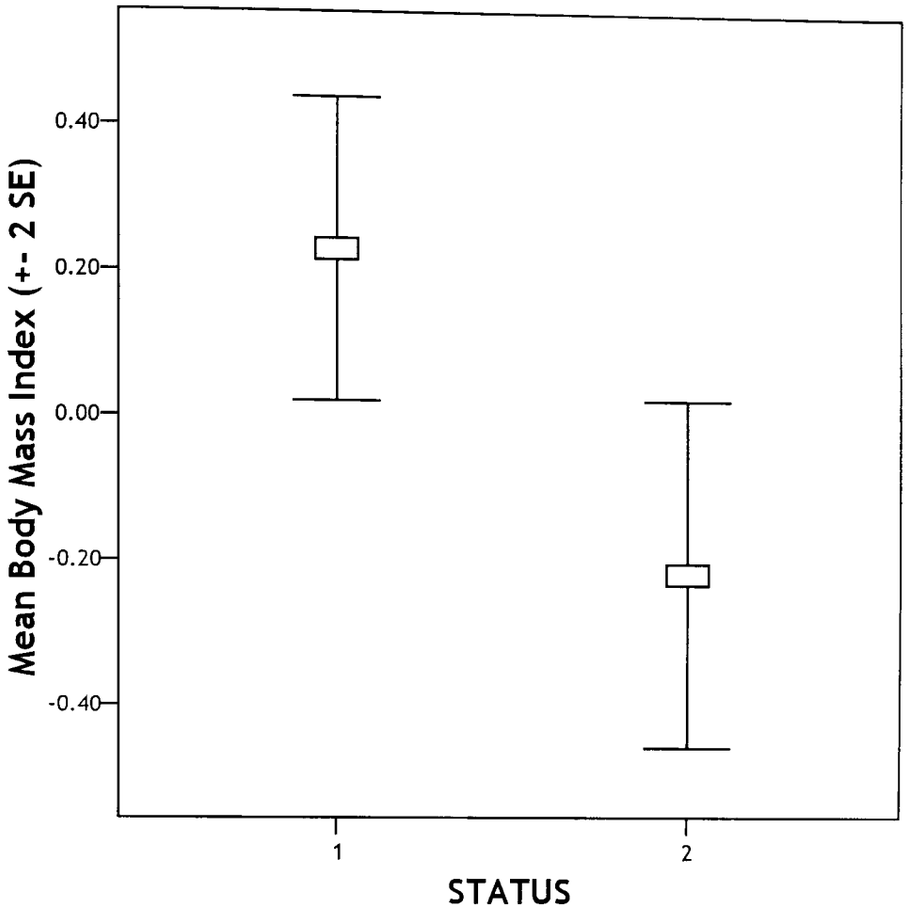


Figure 3.1: Differences in BMI between non-breeders (=1) and breeders (=2) during 2003-04. Mean Body Mass of Non-breeders ± s.d.= 0.23±0.87, N=71; Mean BMI of Breeders ± s.d.= -0.21±1.04, N=75 (females and males are combined in the same analysis).

Seasonal effects

There was no relationship between MCV and date of trapping for both breeders and non-breeders, however the other two measures of body condition showed some effects of seasonality. The PMV was positively related to trap date, birds trapped towards the end of the season had higher values than birds caught at the beginning of the season; this was the case for both breeders (R^2= 0.26, p< 0.001, N=72) and non-breeders (R^2= 0.19, p< 0.001, N=68). On the contrary, BMI was negatively related to date in the season in non-breeders only (R^2= 0.11, p= 0.005, N=70). Non-breeding great skuas caught at the beginning of the season were in better

body condition that birds caught towards the end of both seasons (2003-04).

3.3.2 Long term differences

The data set from the 1980s (1984-1990) included a total of 155 non-breeders and 116 breeders. All the birds were of unknown sex, but I assumed an approximately equal number of males and females. This assumption could probably affect the comparison between years, since I trapped more female breeders than non-breeders.

Biometrics

Non-breeders were lighter and smaller in all the body measures, except for tarsus length (breeders had smaller measures than non-breeders):

Table 3.4: Biometrics of non-breeders and breeders during the 1980s.

	Mean	t	d.f.	p
WEIGHT Non-breeders Breeders	 1314 1381	5.36	268	<0.001
WING Non-breeders Breeders	 415.8 424.8	7.45	267	<0.001
HEAD and BILL Non-breeders Breeders	 109.9 111.5	4.70	268	<0.001
TARSUS Non-breeders breeders	 68.4 67.8	2.35	255	0.02

Body Condition

Residuals of the regression of body mass over body size were used as a measure of body condition (BMI) (R^2= 0.25, p< 0.001, N=253). Body size was

the first factor of a PCA including the following measures: tarsus, wing and head and bill; it explained 50.96% of the variance (it included individuals for which all the body measurements were available).

During the 1980s, breeders were in better body condition than non-breeders (ANCOVA with status as factor, $F_{1,253}=9.82$, $p=0.002$, Figure 3.2). Body size was included as a covariate in the model but it was not statistically significant and was dropped from the final model.

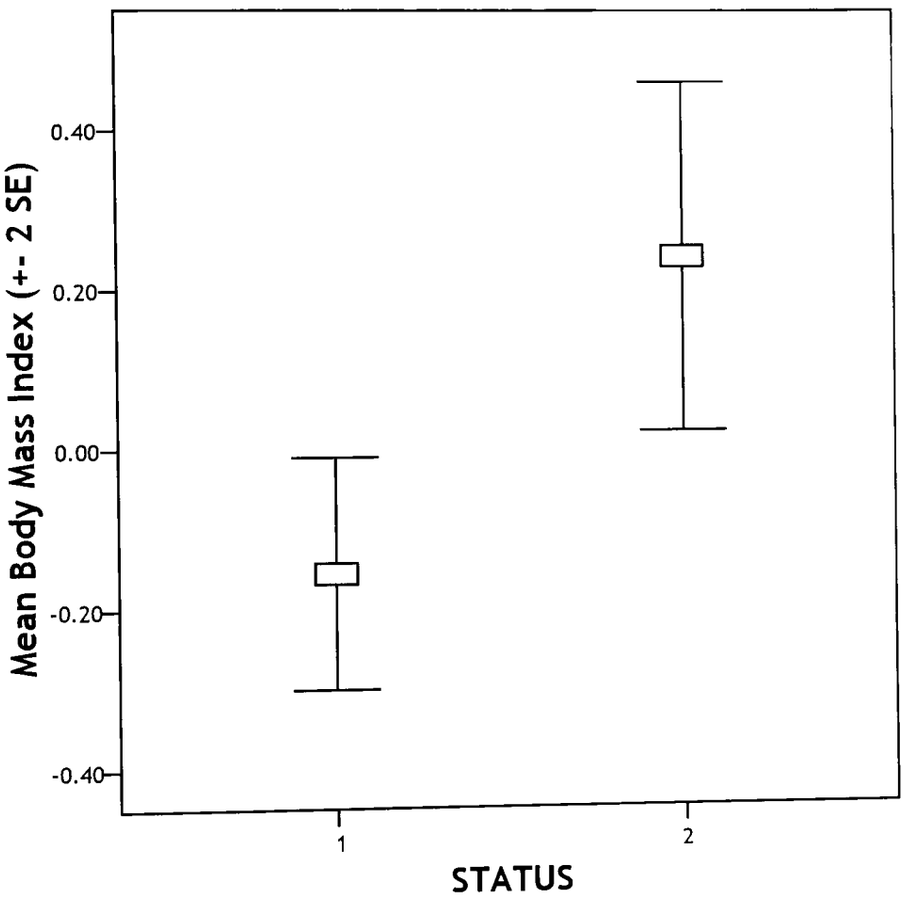


Figure 3.2: Differences in BMI between non-breeders (=1) and breeders (=2) caught on Foula during the 1980s. Mean Body Mass of Non-breeders ± s.d.= -0.15±0.90, N=154; Mean BMI of Breeders ± s.d.= 0.24±1.09, N=99.

3.3.3 Comparison between years

There were fewer data available from the 1970s (1974 and 1976), but it is still possible to analyse body condition, although there is no information about their status and it is therefore difficult to separate between breeders

and non-breeders. To compare between all available years (1974-2004), the residuals from the regression between body mass and wing length were used as BMI (R^2=0.205 p<0.001, N=436).

Birds in the 1970s were in better body condition than in later years, and birds in 2003-04 were in better body condition than birds in the 1980s (ANOVA: $F_{2,433}$=9.40, p<0.001; Figure 3.3), this analysis included both breeders and non-breeders.

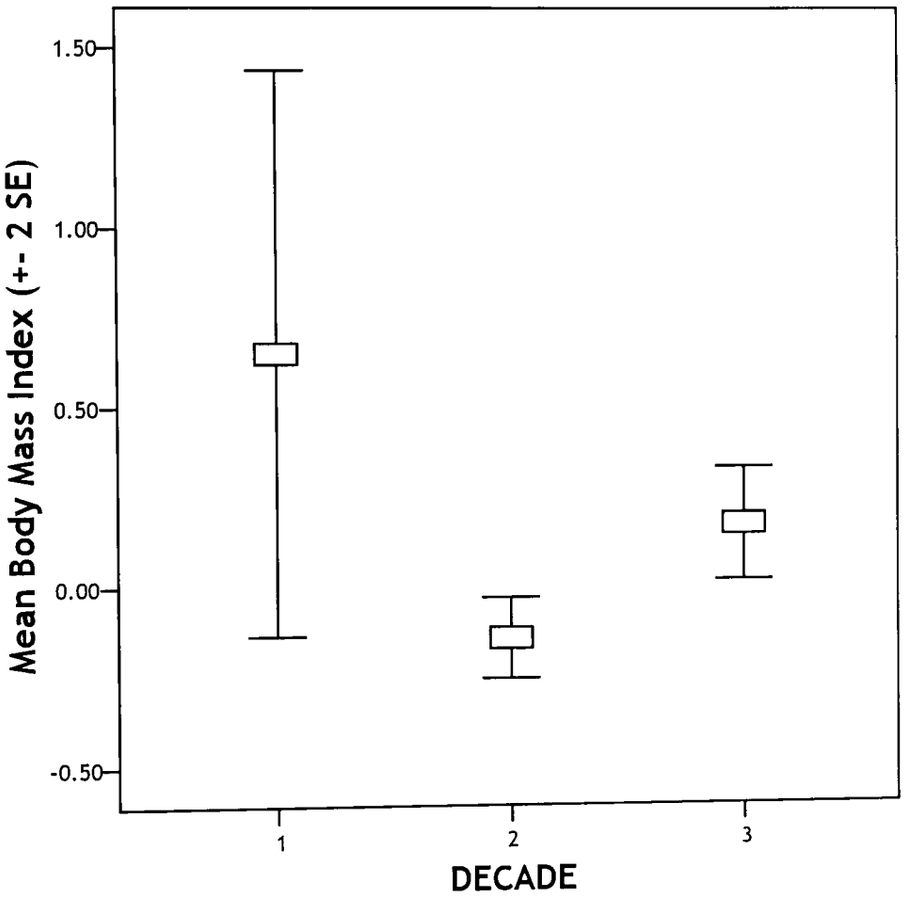


Figure 3.3: Differences in Mean BMI of birds caught in Foula during the 1970s (=1), the 1980s (=2) and 2003-04 (=3). Mean BMI± s.d.: 1970s=0.65±1.71, N=19; 1980s=-0.14±0.92, N=268; 2003-04=0.17±0.95, N=149.

3.4 DISCUSSION

3.4.1 Body Size

From all the body measures taken, wing length was different amongst breeders and non-breeders, although only significantly in males. Also, in females, breeders had on average larger sternum length, however the analysis was not significant. It is possible that on average non-breeders are smaller due to the fact that younger birds visit the club sites. Klomp and Furness (1992) found that among non-breeders visiting club sites within the Foula colony, age varied between 2 to 8 years old. Younger non-breeders may not have fully achieved their adult plumage or size by the time they reach the club sites and this might be responsible for these results. Although this is not clear from this study since we do not have the age of all birds visiting the clubs. Also, birds do not return to the colony during their first year, therefore it could be expected to find only birds that have fully achieved an adult size. It would be interesting to analyse body size in relation to age in order to understand possible differences like the ones in the present study. Therefore, the differences in size between breeders and non-breeders could reflect that there is a selection for bigger individuals amongst prospectors, where only birds of a certain size are able to become breeders in a colony like Foula (highly populated).

In females, non-breeders were on average heavier than breeders (i.e. body mass). This result, does not necessarily indicate that non-breeders are of better "quality" or in better body condition than breeders, because this measure is not corrected for size and it may vary even with daily food intake. Breeders in this study were captured on their nests while incubating (see Methods), so the measures were taken when females had already laid at least one egg. The difference in weight between breeders and non-breeders could be the result of female breeders being lighter after laying eggs. Body mass could also vary between breeders and non-breeders because of their foraging patterns, breeders take turns to forage and care for the nest with their partners (females sometimes get fed by males), but

it is not clear when non-breeders make foraging trips. Therefore it is not appropriate to use body mass as a measure of quality or condition even between individuals with the same status (breeders or non-breeders).

3.4.2 Body Condition

From the three measures of body condition taken, the MCV did not explain differences between breeders and non-breeders. The mean corpuscular volume has been considered a measure of individual condition that could recognize poor quality individuals affected for example, by periods of stress (Bearhop et al. 1999). In the present study no difference was found between the MCV values of great skua breeders and non-breeders attending the Foula colony in 2003. In previous studies, this condition measure has reflected differences in individual quality in relation to colony size (Votier et al. in press), which could indicate that birds present in the same colony are subject to the same competition pressure and they maintain similar levels of stress; thus breeders and non-breeders of the same colony may not necessarily differ in MCV.

According to previous studies, it is expected that non-breeders and/or prospectors are inferior in condition (could mean size), than breeders already holding territories, and that it is a pre-requisite for recruitment to achieve a certain body condition threshold which enables birds to compete for nest sites in large colonies (Wooller and Coulson 1977; Porter 1988; Spear et al. 1995). The prediction for this study was that the three body condition measures used would reflect that breeders are in better body condition than non-breeding birds attending club sites. What I found in this study was the opposite, the PMV showed that in 2004 breeders had lower values than non-breeders (although not statistically significant), one explanation could be that breeders were allocating protein to egg production, therefore their values were lower than non-breeders'. Also, the combined yearly analysis (2003 and 2004) of BMI showed that non-breeders were in better body condition than breeders. This measure of condition is

corrected for body size, and it is an indicator of lipid storage that could be directly influenced by the birds' food intake over a longer period of time. Potential differences between breeders and non-breeders could be due to the fact that both groups are subject to different challenges regarding energy expenditure. For instance, breeders invest in reproductive activities (territory defence, egg laying, incubation, etc.) and non-breeders invest in prospecting activities (territorial aggression, habitat surveying, competition, etc.). It would be difficult to prove that either reproduction or prospecting is more costly than the other because it is a difference in "currency". Thus, to assess if established breeders are "better" than prospective breeders, and whether non-breeders need to achieve a level of condition to become a territory holder in the colony, body size could be a better parameter to measure. Also, if enough data is available, variables such as hatching date and birth colony/site could be used as measures of individual quality.

Although we found no effect of trapping date in body condition of breeders, there was an effect on non-breeders. Also, in 2004 breeders were caught on average earlier than breeders but the difference was not significant. Even if we found no statistically significant differences in the trapping dates of breeders and non-breeders, it would be ideal to obtain all the body measures of both at the same time (at arrival to the colony, before egg-laying). This way birds would not be subject to the effort of reproduction and prospecting and a more accurate measure of "quality" of the birds could be obtained. Unfortunately for practical reasons it is not always possible to trap many birds at the same time.

Yet, it is possible that individual condition of great skuas is related to the current conditions experienced by the colony in terms of food abundance. The two seasons covered in this study (2003 and 2004) were particularly adverse in terms of food availability, according to fishing records, the total sandeel biomass and the combined discards of haddock and whiting were lower during this period than there have been for the last 30 years in the

Shetland region (Chapter 2). Although great skuas exploit different food sources including sandeel, fisheries discards and other seabirds (Votier 2001, 2003), they are vulnerable to fish abundance (Votier et al. 2004c). Certainly, both breeders and non-breeders would have been affected by the adverse foraging conditions, but breeders in addition to providing for themselves, also incur costs in reproductive behaviours such as territory maintenance and egg production which have been demonstrated to be costly (Kalmbach et al. 2004). It is important to consider that the BMI of breeders could be affected by reproductive effort, and therefore not comparable with the BMI of non-breeders. Since the sample of breeders contained more females than males, and their body condition is directly affected by laying eggs, the differences in body condition found between breeders and non-breeders could be due to the effect of reproductive effort.

The effects of reproduction did not only impact on body condition but on the breeding success as well. During 2003 and 2004 laying date was on average later than in previous seasons and there were fewer chicks produced per nest (Mavor et al. 2005). Non-breeding great skuas attending club sites could be in better body condition than known breeders holding territories because of the particular conditions of the season (i.e. low food availability), and this could be more evident in highly competitive colonies like Foula, Shetland.

In contrast, analysing a data set from the 1980s of Foula breeders and non-breeders (see below), it showed that breeders were in better body condition than non-breeders, as reflected by the BMI. The environmental conditions during the 1980s changed substantially; but even though there was a decline in the numbers of sandeels and discards at the end of the decade, for most part of this period environmental conditions were favourable for birds and they were reflected in high breeding success of the colony (Chapter 2). Under those circumstances the quality of the individuals represents an important factor for recruitment, so breeders would be birds in better body condition whereas non-breeders would need

to achieve a certain level of body condition to be able to obtain a territory and a breeding partner.

3.4.3 Long-term body condition

After analysing three different sets of data (1970s, 1980s and 2003), I found that great skua body condition (i.e. BMI) declined in the Foula colony from the 1970s to the 1980s. Also I found that birds in 2003 were in better body condition than birds in the 1980s; however they had lower values of BMI than birds in the 1970s. Although the body measures used to obtain the BMI (wing length and body mass) are comparable through years (after fieldwork experience they seem to vary the least between people taking them), the fact that I pooled females and males into the same analysis considering an equal sex ratio could potentially have an effect on the results, yet comparing with data of variation in the food availability and numbers in the colony it is possible to explain the differences in body condition between the decades.

Observing the relationship between food abundance (total sandeel biomass and fisheries discards) over the same period of time (1975-2003) it is possible to see that there has been a decline in the fish stock (Chapter 2). In the same graph (Figure 2.9) it is shown that in the late 1980s there was a decrease in the food availability and that at the beginning of the 1990s the fish stock total recovered. There are some studies that provide evidence of an effect of low food availability on the phenotype of birds, furthermore this effects can affect survival and fecundity. Cooch et al. (1991) found a decline in body size over a long-term study (18 years) in snow goose goslings (*Anser caerulescens*), which resulted in overall smaller adult birds. The reduction in body size was associated to non-genetic factors: adverse weather and a long-term reduction in food availability (Cooch et al. 1991). In another study, Ruiz et al. (1998) found a decrease in body size of Audouin's gulls (*Larus audouinii*) over a 13 year long period, this effect was caused by environmental constraints such as colony density and food availability. In the case of great skuas on Foula it is possible that over the

years the environmental conditions (population density and food availability) have become more difficult for the birds to deal with, and this has had repercussions on their body condition; under these circumstances it is difficult to determine if the differences between breeders and non-breeders are due to quality or to environmental conditions.

Whereas a comparison of body condition (i.e. BMI) between breeders and non-breeders may not provide evidence of "pre-requisites" for recruitment, body condition could potentially be compared between individuals amongst years. Studies like the present one would benefit from databases which include sexed individuals (genetically, by behaviour or by a discriminant analysis) and more consistency of the measures taken (focusing on measurements less likely to vary amongst observers like wing length and body mass). As mentioned before, ideally capturing should be aimed to occur at the same time during the season. That said, the value of this study is that it evaluates previous hypothesis and presents results, which to our knowledge have not been conducted before, due to the practical difficulties of obtaining information from birds before recruiting.

4. Club attendance patterns of non-breeding great skuas

4.1 INTRODUCTION

Age at first breeding is one of the most important life-history traits of an individual. For some species, the decision about the timing of reproduction represents a trade off between reproductive success and long time survival. In birds there is a wide range of ages at which individuals start to breed, and this variation can be different between populations depending on variables such as food availability, colony size and climate conditions. It is well known that long-lived species present delayed reproduction, which means that birds make their first reproductive attempt when more than 2 years old (Furness and Monaghan 1987). Some examples of age at first breeding in seabird species are shown in Appendix 4.1. Young inexperienced birds may be unable to provide for themselves and for the chicks with food and suitable growing conditions at the same time (Lack 1968; Greig et al. 1983), by deferring maturity they are maximizing the number of offspring that can be produced over their lifetime (Nelson 1980). In seabirds, reproductive performance increases with age, at least during the first reproductive years, not breeding at a younger age allows individuals to accumulate resources which will give them future reproductive benefits (reviewed in Forslund and Part 1995; Ratcliffe et al. 1998). In the years prior to breeding, birds would improve in foraging abilities, access to resources and in other reproductive skills.

This experience is obtained as they age, therefore older non-breeders become more active in the colonies and arrive earlier in the season than younger non-breeders. In common guillemots (*Uria aalge*), immatures tend to arrive progressively earlier in the season and visit fewer breeding sub-colonies within a season as they age. Not only do birds spend more time in the colony as they approach recruitment age, but those attending the colony more often both in the year of recruitment and in the previous year are more likely to begin breeding than same-aged birds investing less in colony attendance (Halley et al. 1995). Colony size is another element that influences age at first reproduction, it is possible to expect that in dense colonies the age of first breeding is older than in colonies with lower

numbers of birds. Age at first breeding could also increase with decreasing colony density (e.g. Cassin's auklets *Ptychoramphus aleuticus*, Pyle 2001), although it can also be dependent on food availability (Pyle 2001; see also Western gulls *Larus occidentalis*, Spear et al. 1995).

After the first year of return to the colony, the number of days spent in the colony and the time spent interacting with other birds increases. During these stays they interact with other birds in displays. So, the recruitment rate is related to the experience acquired during visits in previous years (wandering albatross, *Diomedea exulans*; Pickering 1989). Social limitations for recruitment may operate through competition for limited resources in the colony such as territories or nests. In these cases, smaller colonies may provide more opportunities to recruits, and they show a tendency to grow faster than larger colonies (Coulson 1983; Moss et al. 2002). So, social dominance is another factor affecting recruitment, in kittiwakes (*Rissa tridactyla*), dominant birds in better body condition are able to take spaces in highly competed or dense colonies; the patterns of recruitment are related to individual quality and to arrival dates of potential recruits (Porter 1990). Furthermore, kittiwake recruits were at least three years old and they were present at the colony at least one year prior to breeding, they are highly attached to the colony, and this is demonstrated by their early arrival (Porter 1988, 1990).

A common feature found in many seabird colonies is the presence of immature non-breeding birds occupying areas around the nesting sites. These individuals attend the colony every season for one or more years before making their first reproductive attempt (for a review of studies documenting the presence of immatures in colonies, see Danchin et al. 1991). In some seabird species, young adult birds (i. e. non-breeders) settle close to adult nesting areas in delimited locations of the colonies referred to as *clubs*, where they perform social interactions with other birds (Pickering 1989; Klomp and Furness 1990; Bradley et al. 1999). Club sites are prominent at large colonies. The presence and size of clubs depends on the "health" of the bird colony, if a colony is declining there

may be no clubs at all. In large and densely occupied colonies there may be many clubs. Small colonies may have a large club if many birds are colonising the area from somewhere else (Furness 1987). Achieving a breeding status in the colony means that a bird has been recruited into the reproductive fraction of the population, so *recruits* can be defined as birds breeding for the first time in a colony in the current year (Danchin et al. 1991). However, in this study I have defined recruits as birds that succeed in establishing a territory, a clear distinction from being a club member. This definition is more practical in that it is straightforward to identify birds that are holding territory, but more difficult to be certain whether or not these birds have actually bred for the first time. It is sometimes difficult to tell whether a newly established pair in a territory has laid an egg and lost it immediately, which complies with Danchin's definition of recruitment, or whether they have held a territory but not laid an egg.

Among the literature there are several terms to classify status of non-breeding birds present in a certain colony. In general, depending on whether the age of the individual falls into the range of age at first breeding, birds can be either *immatures* or *prospectors*. Immaturity is considered both physiological and/or behavioural, these are birds of a younger age that can not breed yet; on the other hand, prospectors are birds whose age is included in the range of ages of first reproduction (Danchin et al. 1991; Oro and Pradel 2000), who are attending the colony "waiting for a chance to recruit". Prospectors are looking actively for a breeding place, and they may evaluate different colonies in the search for a suitable nesting site. Because of the constraints and restrictions of breeding for young immature birds, delayed reproduction may be caused by the need of individuals to gather information about the suitability of the breeding sites where they can recruit (Curio 1983, Boulinier and Danchin 1997). Through prospecting, birds have the opportunity to assess the quality of potential breeding places.

Great skuas

Great skuas are highly site-faithful as breeding adults and their populations tend to be stable between years (Klomp and Furness 1990). Age at first breeding varies between colonies, but also varies a great deal between individuals. Great skuas show a long period of immaturity approximately 5-8 years old (the oldest maybe 11 years old) (Klomp and Furness 1990).
In great skua colonies, apart from the breeding territories, other gathering sites can be classified into the following: ***bathing sites***, ***club-sites*** and ***temporary clubs*** (Klomp and Furness 1990). Club-sites are fairly evenly spaced through the colony and they are usually 30-70m in diameter (Klomp and Furness 1990). Non-breeding great skuas frequent these club-sites during the breeding season each year, they gather in a flock to rest together or to display and begin to practice agonistic and reproductive behaviour (Furness 1987). Birds attending club-sites are mostly 3-8 years old; great skuas will often occupy a territory for a season before breeding, so that 'recruitment' can be difficult to measure accurately given that their first breeding attempt may well result in early loss of eggs. Great skuas tend to construct several nest scrapes within their territory and it is not easy to be sure whether or not one of these has held an egg for a day or two. Bathing sites are used by both breeding and non-breeding birds, but they usually have a non-breeding component or club associated with them. Temporary clubs are formed towards the end of the season in additional areas, when some territories have been vacated by breeders (Klomp and Furness 1990).

The present chapter examines the current situation of non-breeders in Foula by looking at the attendance patterns of birds at the club sites. It also compares the recent challenging conditions (declining numbers of breeding pairs) faced by the birds to the better conditions experienced in the colony in the past three decades (higher breeding success and higher densities).

4.2 METHODS

Data were collected during the 2003-2005 cohorts and compared with data existing from 1977, 1986 and 1988 already published by Furness (1987) and Klomp and Furness (1990). Since 1977, 11 club sites and 4 bathing sites were recognized (Furness 1987); later in 1988 there were 10 club sites and 4 bathing sites (Klomp and Furness 1990). From 2003, only eight club sites were still being used and four combined bathing and club sites (see Appendix 4.2).

During 2003 (mid May to mid July), 2004 (beginning of May to end of June) and May 2005, club sites were visited and the number of non-breeding birds attending was recorded on each visit. Counts were made at different times during the day from 9.00 to 19.00 hours. Klomp and Furness (1990) reported that the maximum number of birds attending clubs occurred at night, however from my personal observations I gathered that there is no daily pattern of attendance. Some initial sporadic observations were done at midnight but they were not dissimilar to observations done during the day (these counts were anecdotal), therefore regular counts were performed during day time (9.00-19.00). In Foula around summer the sun sets almost at midnight and it rises approximately at 4.00 hrs. and it does not seem to relate to birds' attendance to the colony. Breeders leave on foraging trips early in the morning, leaving their partners attending the nests (J. Crane pers. comm.); however information about non-breeders foraging trips is not available. Another element influencing the presence of birds around the territories is the weather conditions, in dense fog or rain the birds tend to stay at their places regardless of the time of day (pers. obs.).

A large number of great skua breeders have been colour-ringed in Foula during the past decades, therefore it is possible to know the frequency of their visits to the club sites; it is extremely rare to see colour-ringed breeders attending club sites during the breeding season (Klomp and Furness 1990, pers. obs.). Efforts were made to register all colour-ringed birds attending the club sites. Non-breeders were also recognized by their

behaviour on the club sites, birds forming a pair and defending a territory on the edge of the clubs were excluded from the counts. Known breeders were not considered in the number of birds attending clubs, although they may have been part of the counts in bathing sites. In 2003, efforts were made to visit all the club sites several times during the breeding season, in 2004 and 2005 counts were less frequent in all the clubs and focused on two of the largest club sites.

To analyse relationships between variables, linear regressions were used. Statistical analysis was done using SPSS 12 and Microsoft Excel.

4.3 RESULTS

4.3.1 Seasonal and Day-time variation in numbers at club sites

Although the number of birds present in a particular club site varied widely during the daily counts in **2003**, no particular pattern was found when regressing number of non-breeders in a club-site (including combined bathing sites) against time of day from 9.00 to 19.00 hrs. (eight club-sites: $R^2<0.01$ $p=0.91$ $N= 77$ counts, Figure 4.1; four combined club and bathing sites: $R^2<0.01$ $p=0.89$ $N=42$ counts; Figure 4.2). Also, attendance, measured in number of birds present during a certain hour of the day, showed no pattern through the season from May to July. For all club sites, there was no relationship between the number of birds and the day of the year at which counts were made. (eight club-sites: $R^2=0.02$ $p= 0.15$ $N=77$ counts, Figure 4.3; four combined club and bathing sites: $R^2=0.02$ $p=0.30$ $N=42$ counts; Figure 4.4).

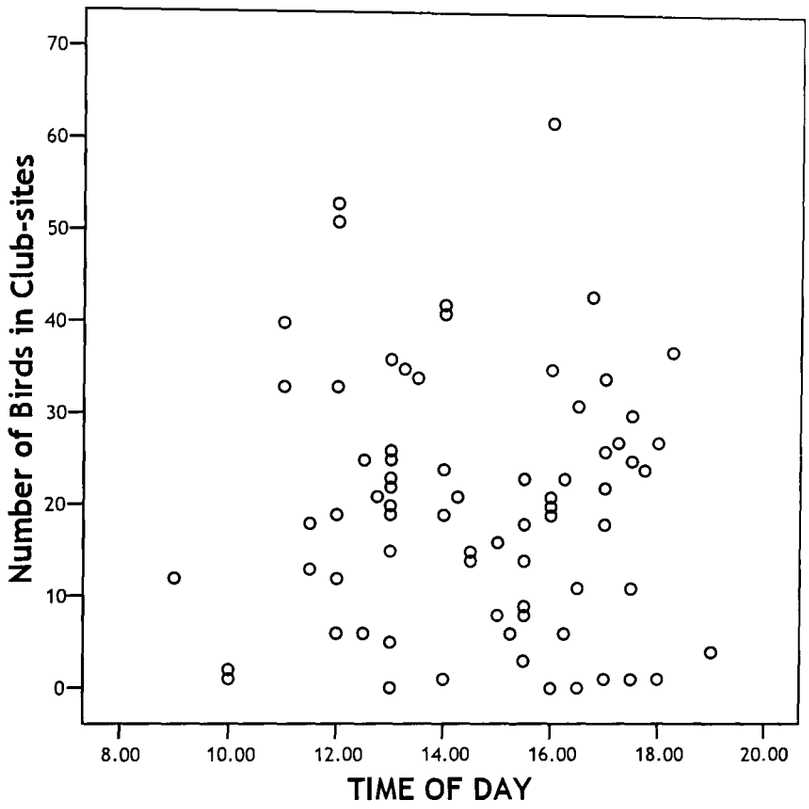


Figure 4.1: Number of birds present on all of the eight club-sites visited during 2003 and recorded time of the count (between 9.00 and 19.00 hrs).

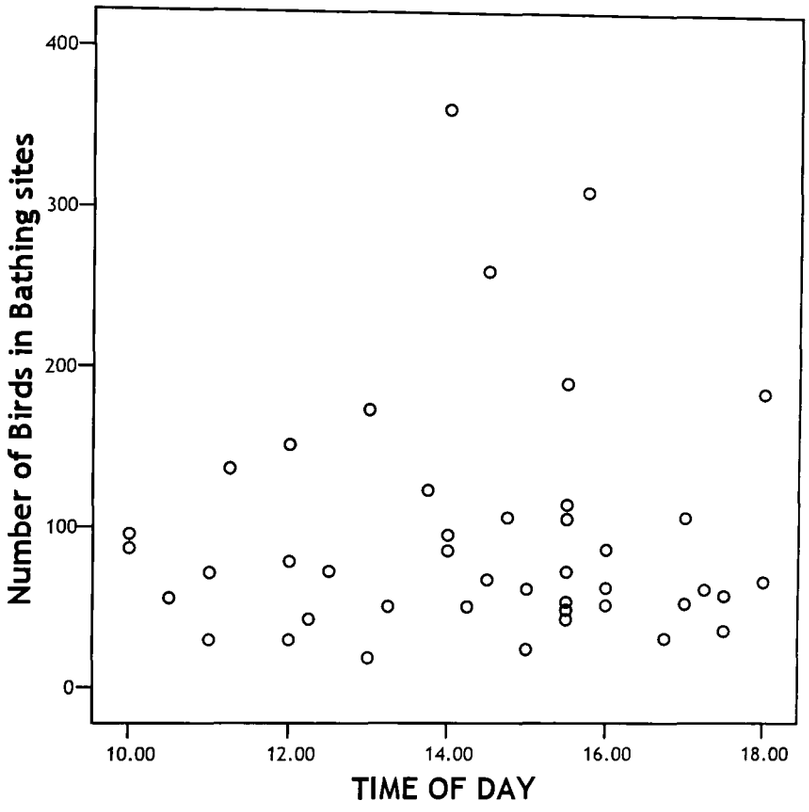


Figure 4.2: Number of birds present on all of the four bathing sites visited during 2003 and recorded time of the count (between 9.00 and 19.00 hrs).

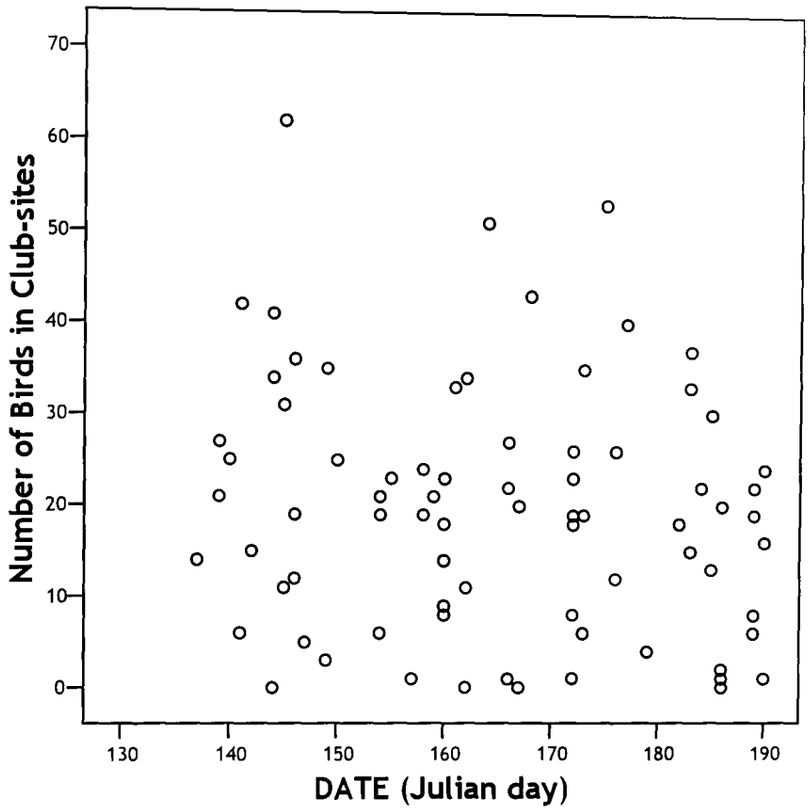


Figure 4.3: Number of birds present on all of the eight club-sites visited during 2003 and date in the season (Julian day, January 1st=1; May 20th=140).

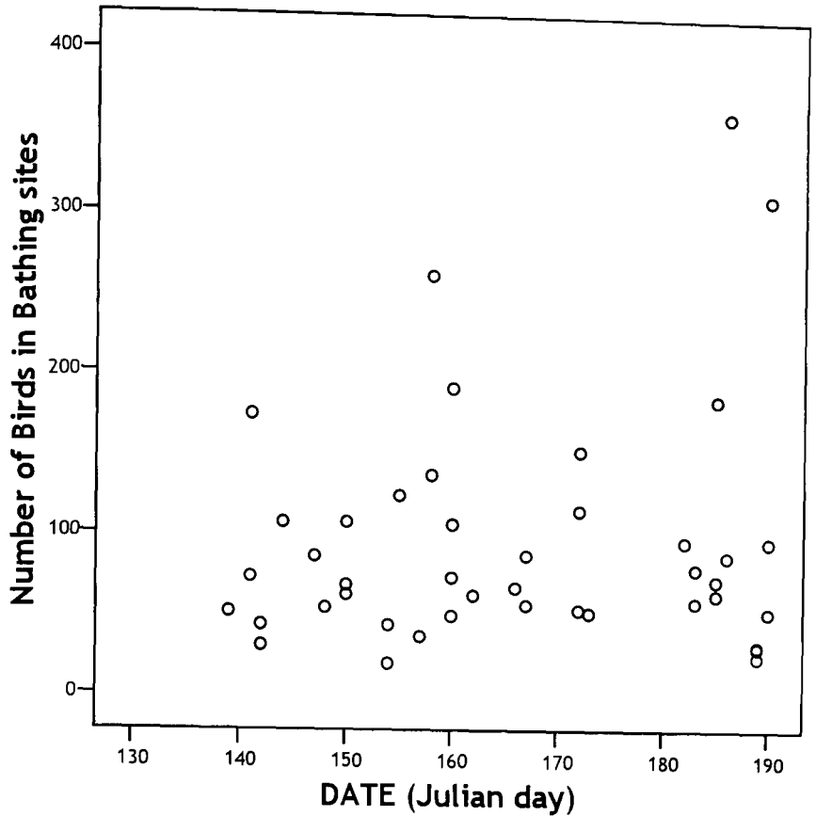


Figure 4.4: Number of birds present on all of the four bathing sites visited during 2003 and date in the season (Julian day, January 1st=1; May 20th=140).

Seasonal comparisons between two club sites

During **2004**, the attendance counts focused on two clubs in the colony (Netherfandal and Strem Ness; Appendix 4.2). In 2004 the numbers of non-breeding birds attending either club site increased as the season progressed (Netherfandal Club: R^2= 0.55 $p<0.01$ N=20 counts Figure 4.5; Strem Ness Club R^2=0.47 $p<0.01$ N=38 counts Figure 4.6) but there was no relationship between attendance and the hour of the day (Netherfandal Club: $R^2<0.01$ $p=0.98$ N=20; Strem Ness Club: $R^2=0.02$ $p=0.42$ N=38 counts). During 2003 there was the same tendency in only one of the clubs (Netherfandal) but the analysis was not significant (Netherfandal Club: $R^2=0.05$ $p=0.39$ N=16; Strem Ness Club: $R^2<0.01$ $p=0.98$ N=26 counts).

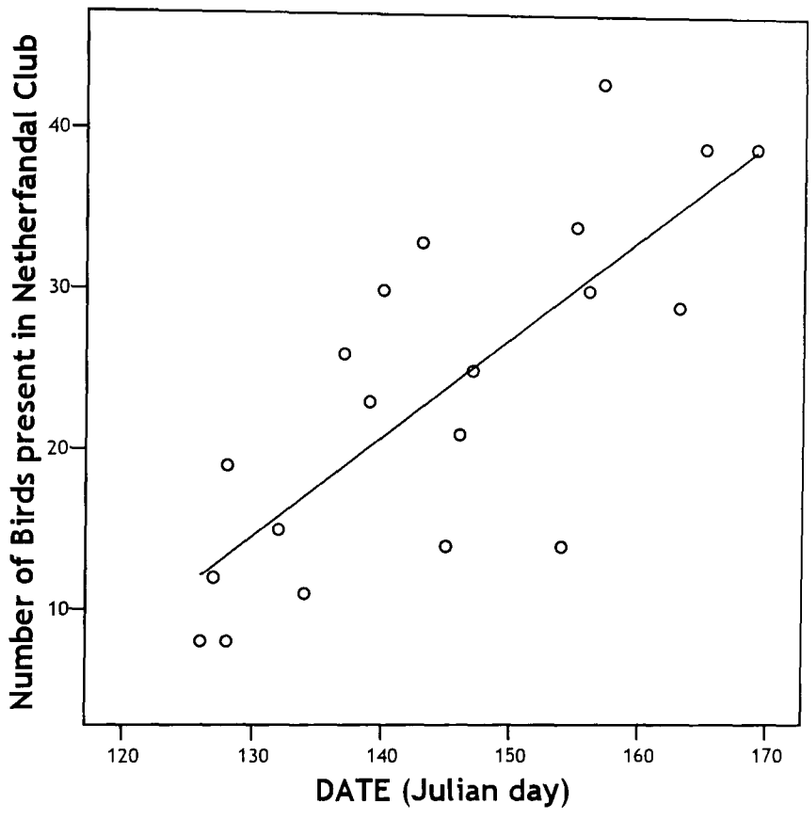


Figure 4.5: Number of birds present on Netherfandal club in each visit during 2004 and date (Julian day, January 1st=1; May 10th=130).

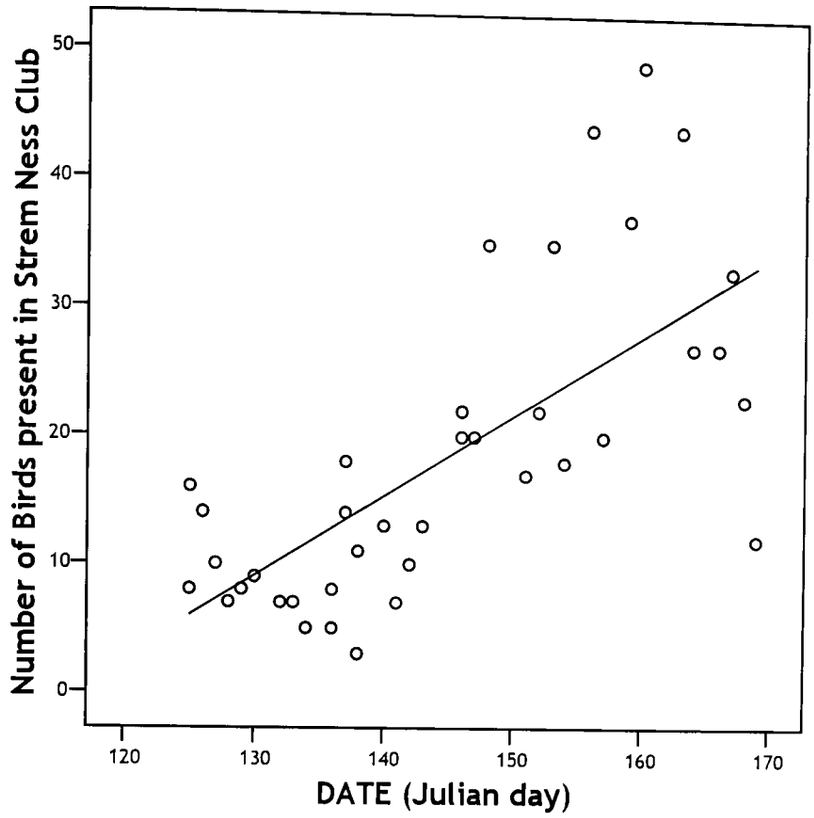


Figure 4.6: Number of birds present on Strem Ness club in each visit during 2004 and date (Julian day, January 1st=1; May 10th=130).

During 2004 attendance to club-sites was apparently lower than in 2003, but this was not reflected in the statistical analysis once time in the season was taken into account. The numbers in one of the two focused club sites were significantly higher in 2004 than in 2003 (see below in Table 4.1 and Figures 4.7 and 4.8) during the month of June. Only comparing counts taken in June was considered to account for the lower numbers of birds attending the clubs at the beginning (May) and the end (July) of the season, so making comparison between years more appropriate given that counts were made predominantly earlier in the season in 2004 than in 2003.

Table 4.1: Average attendance of birds to club sites in 2003 and 2004 (N= number of counts during the month of June).

Club	2003	N	2004	N	t	p
Netherfandal	21.7	7	32.6	7	2.40	0.03
Strem Ness	27.0	17	30.7	12	0.76	0.45

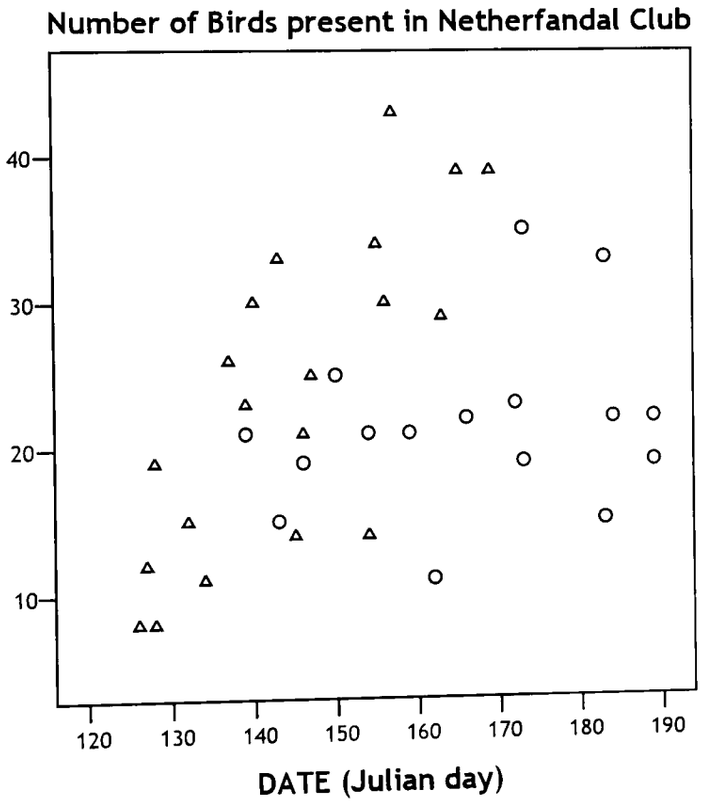


Figure 4.7: Number of birds present on Netherfandal club in each visit during 2003 (○) and 2004 (△); and date (Julian day, January 1st=1; May 10th=130).

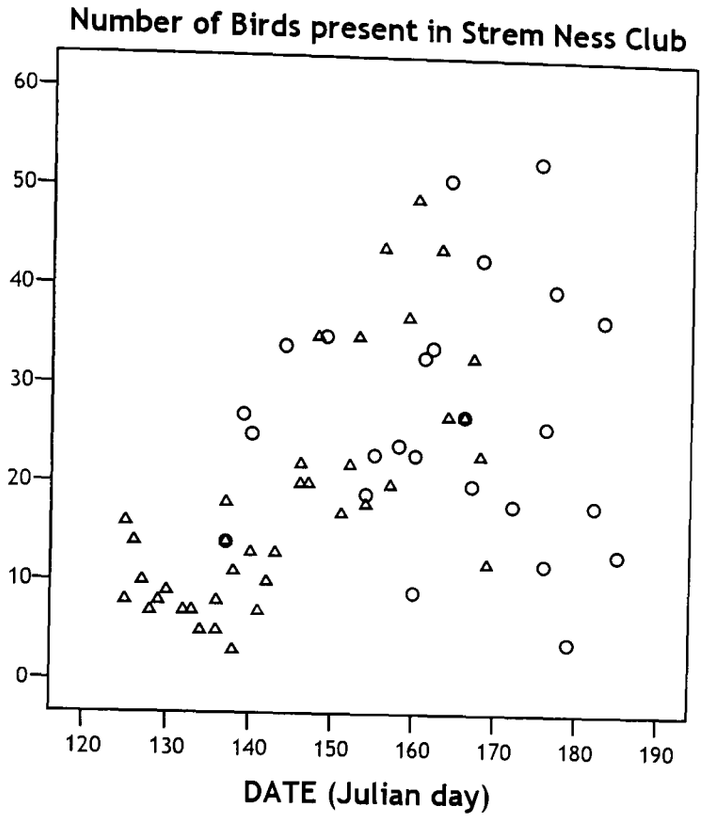


Figure 4.8: Number of birds present on Strem Ness club in each visit during 2003 (○) and 2004 (△); and date (Julian day, January 1st=1; May 10th=130).

4.3.2 Number of birds attending club-sites: long-term comparison

Overall, the total number of non-breeding great skuas attending club-sites at the peak of the breeding season showed a 22.4% decline since 1988 (Table 4.2). Also, from the club-sites described in 1987 and later in 1988, two of them had disappeared by 2003 (Liorafield and South Ness) and some had almost no attendance at all (see Appendix 4.2). Table 4.3 shows counts made in all club sites of the island between 1977 and 2005. Counts were made at different times of day. Counts in 1977 and 1986 were made around seasonal peak of non-breeder attendance during June-July and the numbers are maximum attendance counts (Furness 1987). Data from 1988 was taken on two dates (29th May and 5th June) (Klomp and Furness 1990). Counts from 2003-2005 were made from May to July. Total numbers are provided

only for the years where counts were systematically made in all club sites. In 2004-05 counts were not made in all clubs, therefore data is non-available (n/a).

Table 4.2: Number of non-breeding birds attending individual clubs on a particular day during seasonal peak. Date is 5th June in 1988, in 2003 is the closest day to June 5th (referred as day difference). Counts were made at different times of day.

CLUB	1988	2003	Percentage differences	Day differences
Mill Loch	32	124	+ 287.5	-1
Liorafield	21	0	n/a	n/a
Bottle	21	1	- 95.2	1
Strem Ness	65	23	- 64.6	-1
Noup	30	8	- 73.3	4
South Ness	0	0	n/a	n/a
Hamnafield	43	18	- 5.2	4
Kame	14	23	+ 64.2	4
Flick	108	43	- 60.2	-2
Overfandal	88	106	+ 20.4	4
Netherfandal	38	21	- 44.7	-2
Rossies	32	36	+ 12.5	1
Daal	69	19	- 72.5	2
Smallie	23	31	+ 34.8	-11
Ouvra Valley	0	0	n/a	n/a
TOTAL	584	453	-22.4	

Table 4.3: Attendance of non-breeders to club-sites in different years.

CLUB	1977 (max)	1986 (max)	1988 (June 5th)	1988 (mean 2 days)	2003 (mean)	2003 (maximum)	2004 (maximum)	2005 (maximum)
Strem Ness	220	50	65	64	26	53	49	36
Netherfandal	90	110	38	40	21	35	43	30
Daal	160	80	69	47	29	62	40	n/a
Smallie	0	0	23	29	10	31	n/a	n/a
Hamnafield	250	60	43	31	12	18	n/a	n/a
Kame	130	30	14	17	12	23	n/a	n/a
Noup	120	15	30	28	8	16	7	n/a
Bottle	160	100	21	27	2	6	0	n/a
Liorafield	200	110	21	32	0	0	0	n/a
South Ness	0	10	0	0	0	0	0	n/a
Ouvra Valley	0	0	0	0	0	0	0	n/a
TOTAL	**1330**	**565**	**324**	**315**	**120**	**244**	**n/a**	**n/a**
Mill Loch	180	160	32	47	163	362	123	59
Flick	320	95	108	107	41	51	41	n/a
Rossies	30	40	32	34	60	87	51	31
Overfandal	160	80	88	68	71	115	18	n/a
TOTAL	**690**	**375**	**260**	**256**	**335**	**615**	**n/a**	**n/a**

4.4 DISCUSSION

During fieldwork in 2003-2005, attendance counts of non-breeders on club-sites were not related to the time of day. Each club was visited at different times of the day during the breeding season on several occasions. After analyzing the number of birds present in club sites and the time of day in which the counts were made, no particular pattern was found. Although in a previous study in the late 1980s it was suggested that the majority of birds attending a particular club are present at night (see Methods), the results from this study show that there was no clear relationship between the number of birds and the time of day between 9.00 and 19.00 hours. This was also the case for club-sites associated to bathing sites where the numbers of birds present may vary during the day depending on the temperature (S. Oswald unpublished PhD thesis, University of Durham). Therefore, the maximum number of non-breeding birds attending club-sites at a specific date should not be affected by the time of day they were counted at. Also I have provided an average daily attendance which could be useful when comparing bathing sites since the numbers in those clubs vary the most during the day. When comparing between years, I used counts done around the same date as recorded on previous years, which is approximately at the middle of the breeding season when attendance is at its peak (Klomp and Furness 1990). To compare between years, for conservational purposes it might be useful to count at a specific day in relation to laying date in the colony averaging several counts during one day. Counts are very variable between days and hours of day in the same club, this could be due to weather (periods of fog or hard rain), foraging or disturbance (humans or sheep).

During 2004, the breeding season was challenged by a very low food availability which resulted in low breeding success, the lowest that has been registered for many years (see Chapter 2). This event was also reflected in a later breeding season with laying days shifting a few weeks (personal observation). However, the average number of birds attending two of the major clubs in the colony was higher in 2004 than in 2003. It is

possible that in 2004 birds were gathering in more popular sites since many other clubs had fewer attendants and some sites were even vacant in that season (pers. obs.).

The Foula colony has been studied for more than 30 years, there have been regular counts of the population, and general description of the breeding territories and club sites. In 1977, 12 club sites were recognized, these included all the bathing sites where both breeders and non-breeders gathered during the breeding season (Furness 1987). In later studies of the 1980s, reports showed 13 club and bathing sites, although total numbers of birds attending these sites were greatly reduced (Table 4.3). During the first year of this study (2003) all the locations where previous club-sites were found were visited; most of these clubs had a reduced number of birds attending them and two of the originally described sites were no longer being used as clubs (Table 4.3). All locations used as bathing sites (small lochs) were still being used by both non-breeders and breeders on the island. In 2004, all the club sites were re-visited (although counts focused only on two clubs of the colony); some of the clubs described in 1977 were vacant and the rest had poor attendance of non-breeders. During 2005 there were some observations done, and in this year attendance to club-sites was very poor, but it coincided with a later season with many breeding pairs missing from their territories (pers. obs.). In this year the maximum numbers of birds in the focused clubs were lower than ever registered.

Even though the results show that counts of birds at club-sites are unrelated to time of day, I assumed that the total number of birds could be comparable with results from a previous study in which counts were only made at night. Klomp and Furness (1990) stated that all non-breeders attending the colony at a certain date would be present at night; my experience differed from these results, but it could introduce some "noise" into the analysis when comparing data between years. In order to have a more consistent comparison of the data between years, it would be sensible to "standardize" the way counts are made. In this way the data base would contain counts that were made in a systematic way regardless

of the observer. My suggestion would be to make counts of non-breeders in club-sites after 17.00 hrs, by this time it is possible to assume that birds would have returned from foraging and bathing trips. Regarding the date in the season, the chosen day for counts should be in relation to laying, hatching and/or fledging. I believe it is important to assess the presence of non-breeders before laying (at arrival to the colony) and at peak hatching and fledging (when prospectors could be assessing reproductive success).

It is important to consider that unless there is a complete identification of all the birds within a colony, it would be hard to determine the total number of non-breeding birds attending in a particular season; as mentioned before non-breeding birds prospect in different colonies and movement between colonies is to be expected. In this context it would be very useful to monitor other surrounding colonies for the activity in the club-sites and for the presence of known birds.

Numbers of birds present in the Foula colony have varied slightly during the past decades, having a peak population size in 1985/86 (Furness and Ratcliffe 2004). This study shows that the maximum number of club sites occurred in 1986, which coincided with the peak number of breeding pairs in the colony. Although the population has been relatively stable with a consistent number of breeding pairs, in recent years the environmental conditions have been indicating that this situation could be changing. Klomp and Furness (1992) pointed out that the number of non-breeders present in a colony was related to the general health of the population, in other words that non-breeders are indicators of the well-being of a colony; and they predicted a decline in the number of non-breeders attending the Foula colony based on their results. My data show that up until 2003 there has been a decline of 22.47% in the number of non-breeding birds attending the club-sites of the colony.

So, recently a decline in the number of non-breeders attending the Foula colony has been registered, this could be related to a decline in the number of breeding pairs holding territories but probably more to low food availability. In recent years there has been a decline in both of the main food sources of great skuas, sandeel and fisheries discards (see Chapter 2).

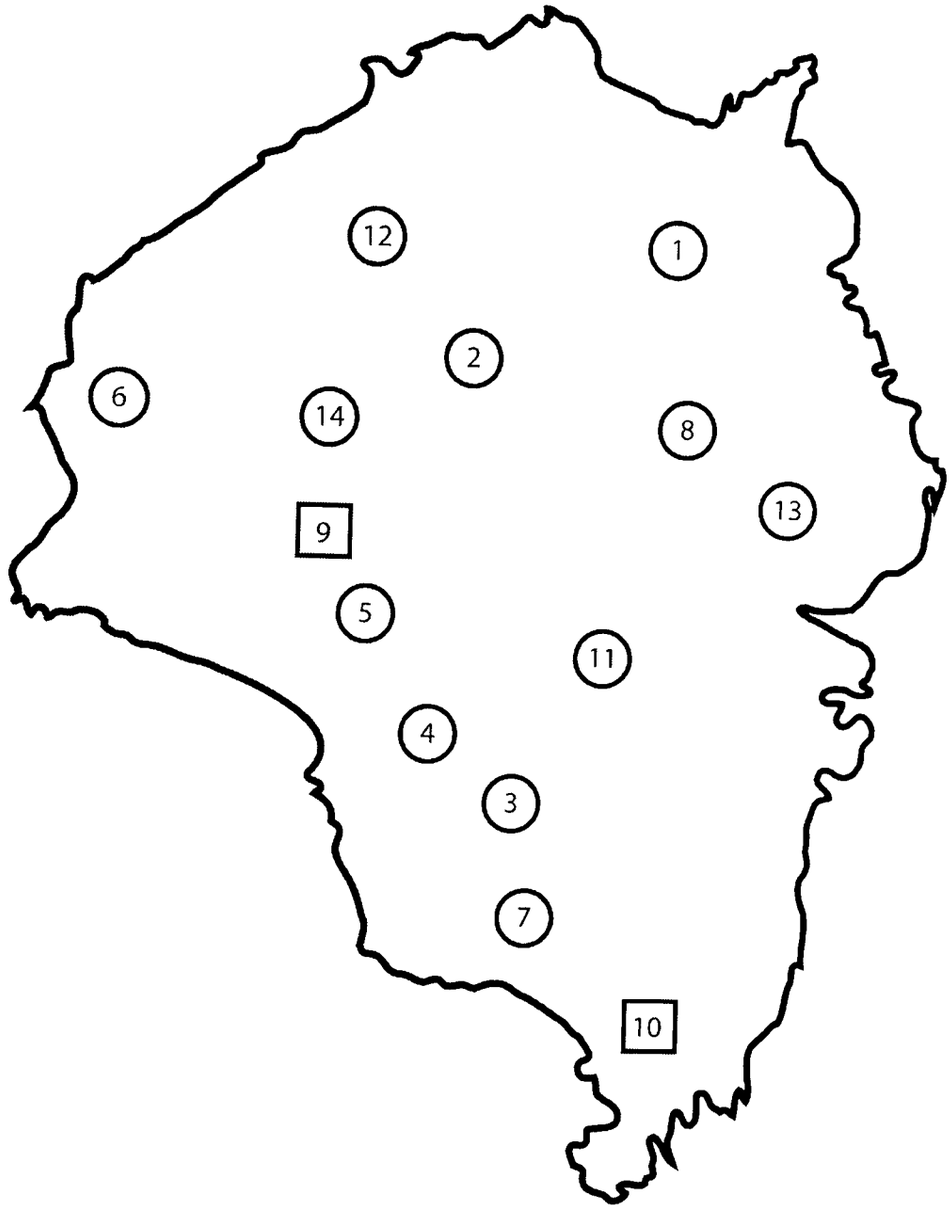
Surely the reduction in numbers of potential recruits would have an effect on the recruitment rates of the colony, whether the shortage in pre-breeders is due to mortality or emigration is yet to be studied, but the results obtained in this study concur with the hypotheses of Klomp and Furness (1992). The impacts of low numbers of non-breeders in Foula could only be assessed if there was a decline in the number of breeding pairs in the colony over the next few years. Also, if there was an increase in the number of newer colonies and the growth of smaller colonies around Shetland and the North of Scotland. It would be very interesting to know whether the recruitment rate in the colony has been related to the number of non-breeding birds present in the colony over the past decades.

Although the methodology used in this study was somewhat different to what was done in the previous study of the same subject, my results provide valuable information in the light of the early hypothesis (Klomp and Furness 1992). Not only did I find that the number of non-breeding birds was declining, I also observed club-sites disappearing (which is unrelated to how the counts were made). It is possible that the effects of low breeding success (Chapter 2) and changes in the breeding population would not be reflected immediately in the number of prospecting birds, but they would certainly change in the coming years.

Appendix 4.1. Age at first breeding in seabird species (extreme ages shown).

COMMON NAME	SPECIES	AGE	References
Wandering Albatross	*Diomedea exulans*	4 to 16	Danchin et al. 1991; Nelson 1980; Pickering 1989
Waved Albatross	*Diomedea irrorata*	4 to 11	Danchin et al. 1991; Nelson 1980
Northern Fulmar	*Fulmarus glacialis*	5 to 19	Danchin et al. 1991; Nelson 1980
Manx Shearwater	*Puffinus puffinus*	3 to 9	Danchin et al. 1991; Nelson 1980
Short-tailed Shearwater	*Puffinus tenuirostris*	4 to 14	Bradley, et al. 1999
Adelie Penguin	*Pygoscelis adeliae*	3 to 7	Danchin et al. 1991; Nelson 1980
Atlantic Gannet	*Morus bassana*	4 to 6	Danchin et al. 1991; Nelson 1980
White Pelican	*Pelecanus erythrorhynchos*	3	Nelson 1980
European Shag	*Phalacrocorax aristotelis*	3 to 4	Nelson 1980
Great Cormorant	*Phalacrocorax carbo*	2 to 3	Nelson 1980
Arctic Tern	*Sterna paradisea*	3+	Nelson 1980
Sooty Tern	*Sterna fuscata*	3 to 10	Danchin et al. 1991; Nelson 1980
Common Guillemot	*Uria aalge*	4 or 5	Nelson 1980
Cassin's Auklet	*Ptychoramphus aleuticus*	2 to 9 males 2 to 10 females	Pyle 2001
Atlantic Puffin	*Fratercula arctica*	6	Nelson 1980
Arctic Skua	*Stercorarius parasiticus*	3 to 7	Nelson 1980; Furness 1987
Brown Skua	*Stercorarius antarctica*	6+	Nelson 1980
South Polar Skua	*Stercorarius maccormicki*	3 to 9	Danchin et al. 1991; Furness 1987
Great Skua	***Stercorarius skua***	**3 to 8**	**Furness 1987**
Black-legged Kittiwake	*Rissa tridactyla*	3 to 8, mostly 4 to 5	Wooller and Coulson 1977 * males breed one year earlier than females
Herring Gull	*Larus argentatus*	4 to 5	Chabrzyk and Coulson 1976 *in dense colonies at 3 years old
Black-headed Gull	*Larus ridibundus*	2 to 5	Prevot-Julliard 2001
Western Gull	*Larus occidentalis*	4 males 5 females	Spear et al. 1995 *modal age shown

Appendix 4.2: Map of Foula showing the location of club and bathing sites.



Club sites: 1. Strem Ness, 2. Netherfandal, 3. Daal, 4. Smallie, 5. Hamnafield, 6. Kame, 7. Noup, 8. Bottle, 9. Liorafield, 10. South Ness
Bathing sites: 11. Mill Loch, 12. Flick, 13. Rossies, 14. Overfandal
In **circles** are the clubs used in 2003 and **squares** are vacated sites previously described. In 2004 site no. 8 (Bottle) was not used as a club.

5. Prospecting and recruitment of great skuas in Foula

5.1 INTRODUCTION

Recruitment occurs when individuals that have not bred before join the breeding fraction of a population. In this study I define recruitment as the establishment of a breeding territory within the study colony by a pair of birds, even if they do not necessarily lay eggs in that season. It is well known that in the majority of seabird species, individuals return to their colonies after one or more years spent at sea. The period of time before breeding for the first time varies depending on different physiological, environmental and social factors. Recruitment can occur to the natal colony (local recruitment) or to another population (i.e. immigration). The time spent by non-breeders in a colony (or colonies) before recruiting is called "prospecting", it is assumed that birds assess the colonies before they decide where to breed. Several hypotheses have been proposed to explain the choice of where to join the breeding population: the conspecific attraction hypothesis (Stamps 1988) assumes that pre-breeders use the presence of breeders of the same species as a cue in breeding-habitat selection thus, dense populations or large colonies attract many new breeders; the conspecific reproductive success hypothesis (Boulinier and Danchin 1997) states that pre-breeders prospect in several breeding patches and preferentially settle in those where reproductive success is high, normally in the subsequent breeding season (Frederiksen and Bregnballe 2001).

In kittiwakes (*Rissa tridactyla*), breeding success and probably other factors such as social behaviour, attract prospectors; which in turn actively participate in colony dynamics making it increasingly attractive. The attendance of prospectors reaches a maximum during the period of highest breeding activity in the colonies, this is when birds can acquire the best information on the quality of the breeding spaces (Cadiou 1999).

Immature birds tend to arrive progressively earlier in the season as they age, and could be seen at the colonies more often as the recruitment time approaches. Older immature birds may visit fewer breeding sub-colonies within a season compared to younger birds. Not only do birds spend more

time attending their colony as they approach recruitment age, but those present at the colony more often both in the year of recruitment and in the previous year are more likely to begin breeding than same-aged birds investing less in colony attendance (Halley et al. 1995). In common guillemots (*Uria aalge*), individual condition is reflected in high colony attendance at early ages, experience and early recruitment (Halley et al. 1995). Another example is short-tailed shearwaters (*Puffinus tenuirostris*), where there is an inverse relation between the age of prospectors and arrival to the colony (Bradley et al. 1999). Some young birds while prospecting in the colonies may occupy unattended nests or chicks from unattended nests which are not their own, these have been called "squatters" and their behaviour is also associated with age (Cadiou et al. 1994).

A number of variables affect the process of recruitment. These variables include colony density, food availability, parental quality (hatching date and order, brood size) and body condition. Colony space is an important determinant of recruitment; often birds tend to be philopatric (i.e. return to breed to their birth colony), but where there is a dense population finding a suitable place to breed becomes a challenge for young birds, in these occasions the outcome may be to delay reproduction or the emigrate to another colony. Studies of the Audouin's gull (*Larus audouinii*) support the idea, showing a relationship between colony size and the probability of any individual to have previously bred at the colony (Oro and Pradel 2000). Also, large colonies are perceived as high quality sites and are actively competed for by prospectors. Only individuals in good condition or more experienced birds can gain territories in such colonies.

Early hatching is correlated with survival after fledging (Spear and Nur 1994), and also makes birds more dominant over late hatched birds, in other words early hatched birds are in better condition than late hatched birds. Amongst the different reproductive variables, hatching date explains variation in recruitment probability. There is a higher recruitment probability of birds with early hatching dates (Coulson and Porter 1985,

Dzus and Clark 1998, Dawson and Clark 2000); also the age at first breeding is negatively correlated with the hatching date of individuals: individuals hatched earlier in the season start breeding at a younger age than individuals born later (Prevot-Julliard et al. 2001). Again, birds may not recruit early at their birth colony, however they may emigrate to breed in less competitive colonies. Environmental variables such as food supply are expected to impact recruitment rates: in good years (high food availability) the age of recruitment could be reduced, whereas in bad years the probability of recruiting may be low (Spear et al. 1995).

An implicit factor in all these characteristics is the body condition of the potential recruits. Body condition of potential recruits is thought to be an important element during the recruitment process (Porter 1988). Birds in better condition are expected to recruit more rapidly and efficiently into the breeding fraction of the population than their counterparts. The quality of the prospectors could be related to their experience i.e. age or to the conditions in which they were reared. Traits such as brood order and hatching date may be reflected in later recruitment success. Accordingly body condition of potential breeders is also likely to be correlated to early recruitment, birds in better condition are thought to recruit more likely than prospectors of poorer condition and also they are likely to nest in higher quality areas of the colonies.

Porter and Coulson (1987) found that there were differences in the body size of prospectors and recruits, which may indicate a considerable competition amongst potential recruits for nesting spaces, in which larger size was advantageous (Porter and Coulson 1987; Cadiou et al. 1994). In kittiwakes, recruits are heavier than prospectors, which may imply that they are in better body condition. Porter and Coulson suggested better body condition as a pre-requisite for recruitment, with another requisite being the age of potential recruits. Recruits would have had at least one year of prospecting before recruiting, during this time birds learn foraging and social skills, thus having the necessary experience at the time of breeding, and they show a high degree of attachment to colony.

In kittiwakes, higher quality birds (i.e. in better body condition) appear to take nest sites in dense areas of their colonies, they are highly competitive individuals that are able to compete even with previously established pairs which tend to be very aggressive towards birds attempting to establish a territory close to them. Time of arrival is an important factor when competing for nest sites, recruits arriving later face higher levels of aggression (Porter 1990).

Furthermore, Porter (1988) suggested that the difference in individual quality causes the variation in the age of first breeding. Considerable selection of individuals at the time of recruitment indicates that new breeders must arrive early in the season and show nest site tenacity.

However, environmental conditions may change through the years even from one season to the next. For example, in cases of increased mortality more nest sites could become vacant and available for new recruits. Porter (1988) suggested that there is a pool of potential recruits from which the new recruits could be selected; in adverse years younger birds may have the chance to join the breeding population. The size and variation of the non-breeding pool is an indicator of the well-being of a population, this can change several years before the breeding population numbers are modified (Porter and Coulson 1987; Klomp and Furness 1992).

Great skuas

Non-breeders settle at traditional conspicuous club-sites spread out around the colonies, mixed with the breeding territories. Age at first breeding can vary between colonies and individuals, great skuas show a long period of immaturity of approximately 5-8 years (the oldest maybe 11 years old; Klomp and Furness 1990). The typical age of the birds frequenting club sites is 3, 4 and 5 years old. Great skuas often occupy a territory for at least part of a season before breeding (Furness 1987; Klomp and Furness 1990). Flexibility of recruitment age depends on availability of territories and other resources; recruitment is responsive to density-dependent influences (Furness 1987).

The small island of Foula located at the north of the British Isles holds the largest colony of great skuas in the world. Records from the colony show a steady increase in the number of breeding pairs from 1900 until the late 1970s; however more recently environmental conditions brought the population growth to a halt. During the late 1980s and early 1990s some studies were done with non-breeders attending club sites, however the recruitment process has not been fully studied within this colony. In the present chapter I relate body condition of the non-breeders to territory acquisition and recruitment in an effort to understand whether differences in individual condition play a role for birds breeding for the first time. Relatively poor environmental conditions (low food abundance and lack of space resulting in nesting at higher density than is typical for the species) and a decline in breeding numbers at this large colony seem likely to make recruitment particularly difficult, and so it was anticipated that differences in recruitment performance of individuals would be particularly evident. Based on previous studies, I would expect to find individuals in better body condition to obtain a territory and attempt reproduction whereas birds of poorer condition would remain in club sites. Considering colony size in Foula and population numbers in the last decades, I could expect a density dependent effect in the probability of recruitment.

5.2 METHODS

Fieldwork for this study was conducted during 2003, 2004 and 2005 breeding seasons in the Foula colony. During the first year of fieldwork, two club-sites on the island (Netherfandal and Strem Ness, see Appendix 4.2) were visited regularly to assess non-breeders' behaviour and numbers. Based on these observations, remotely controlled traps were set. In 2003 and 2004, non-breeding great skuas were trapped using a camouflaged radio controlled spring trap or a string controlled net powered by elastic, with bait to attract birds into the trap. Trapped birds were assigned a unique combination of plastic colour rings; also a metal BTO ring was placed when missing. Several body measures were taken (±0.1mm): tarsus,

tarsal bone, head plus bill, wing and sternum length, and body weight (±10g). Blood was collected from the tarsal vein and was frozen in an eppendorff plastic tube containing EDTA and then used for sexing using the method described by Griffiths et al. (1998) of sex identification (see Chapter 3). During 2004 and 2005, regular observations were done amongst the breeding territories and gathering areas to look for colour rings; the club sites where the trapping was done were visited daily, often twice a day to check for colour rings of revisiting birds. As part of a bigger study, survival and success of breeding birds was recorded; large breeding areas on the island were mapped and colour ringed great skua breeders located on their territories, productivity was recorded regularly, obtaining laying dates and breeding success (number of hatchlings). Great skuas are highly site faithful, so every year they return to the same spot to breed (Catry et al. 1997). Information gathered on the data base for many years made it possible to locate many new birds in between known-birds' territories, and observe their behaviour, many of them were birds trapped on the club sites. Based on their behaviour, colour ringed non-breeders trapped on club-sites were assigned a "status" category (see 5.2.3), also birds were divided into two categories depending whether they returned to the colony or not (see 5.2.2).

Statistical analyses were done using SPSS 12. I used chi-squares to test for differences between male and female return rates. To look at differences between body condition between sexes, I used t-test. To analyse the relationship between body condition and status and fate I used Analysis of Variance; I included body size as a covariate but it was not significant so it was dropped from the final model. Data were checked for the assumptions of parametric tests.

5.2.1 Body Condition

The measure used for body condition was a body mass index, derived from the linear regression between body weight and body size (males: $R^2=0.32$, $p<0.001$, N=37; females: $R^2=0.11$, $p=0.05$, N=34). I used the residuals of this

regression as an individual measure of body condition. Body size was the first factor extracted from a Principal Components Analysis (PCA) of the following body measures: tarsus, head and bill, wing and sternum length (49.62% of variance explained for males and 45.11% for females).

5.2.2 Fate

The seasons following trapping non-breeders at club sites, observations were made around the colony in search for birds carrying colour rings. Birds were divided into two categories: seen (on territories or club-sites) and not seen. Birds that were seen around the colony were given a status based on their behaviour (see below), for birds that were not seen their fate remains unknown (they either died or moved to another colony).

5.2.3 Status

Non-breeders that were re-sighted in the season after being trapped were divided into two categories: club attendants and territory holders. Club attending birds were seen, usually more than once, present at the club site where they were trapped in the previous season. Territory holders were birds that appeared to be holding a territory within breeding territories of the colony, these sites were visited several times during the season and birds were constantly defending the same site.

5.3 RESULTS

5.3.1 Number of Non-breeders trapped in club sites on Foula during 2003 and 2004.

In 2003, 42 non-breeding birds (24 males and 18 females) were trapped in club sites; 30 birds were seen the following year either as territory holders or as club attendants, these birds were also followed another year (2005) but only 16 of them were present in the colony.

In 2004, 29 non-breeders (13 males and 16 females) were trapped in club sites, and 15 of them were seen the following year attending the colony (Appendix 5.1; see also Table 5.2).

5.3.2 Fate of Non-breeders one year after trapping.

There was a higher proportion of birds returning to the colony in 2004 than in 2005. In 2004, approximately 70% of the birds trapped the previous year were seen again in the colony whereas in 2005 only 50% of the non-breeders trapped were seen again.

The proportion of males that were seen again around the colony the following year after being captured in the club sites was similar in both years (62.5% returned to the colony in 2004 and 69.2% in 2005); however this was not the case for female non-breeders, the prospect of returning to the colony lowered dramatically from one year to the next (83.3% returned to the colony in 2004 and only 37.5% were seen in 2005), this difference was statistically significant (x^2=7.53, p=0.006).

Although there seemed to be a difference in the return rate between males and females, the sex ratio of birds sighted around the colony one year after trapping did not differ in either year (2003-2004: x^2=2.18, p=0.14, Figure 5.1; 2004-2005: x^2=2.89, p=0.09, Figure 5.2), possibly due to the relatively small sample sizes involved.

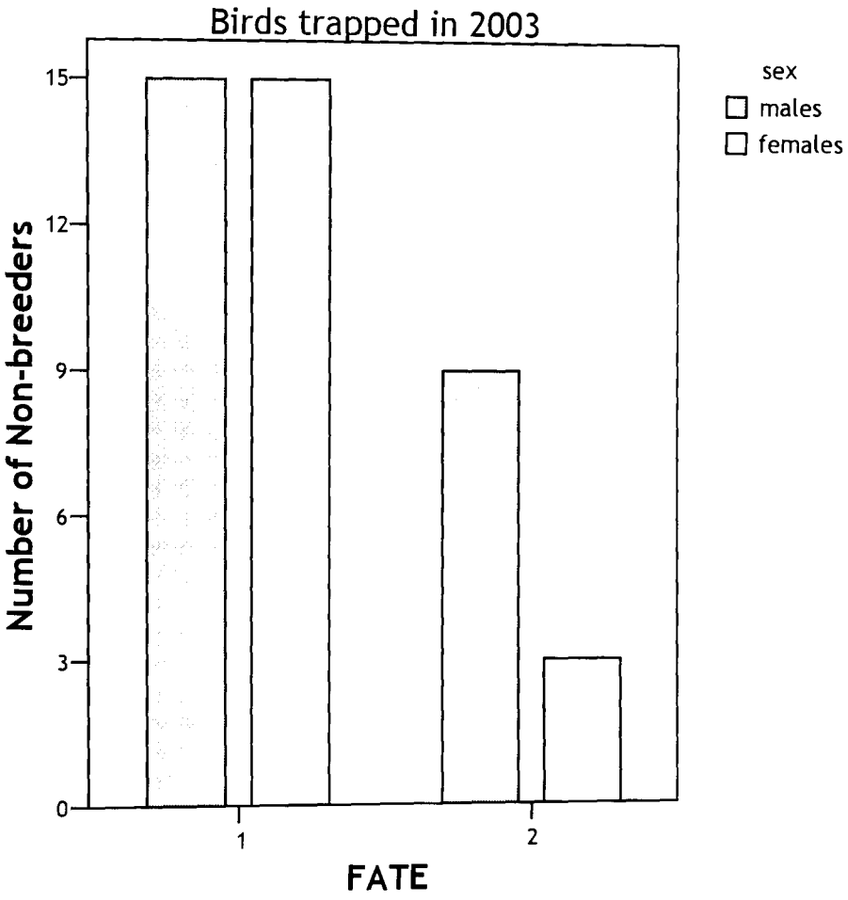


Figure 5.1: Number of male and female Non-breeding great skuas caught on Foula in 2003 and their fate in the following year (1=seen, 2=not seen).

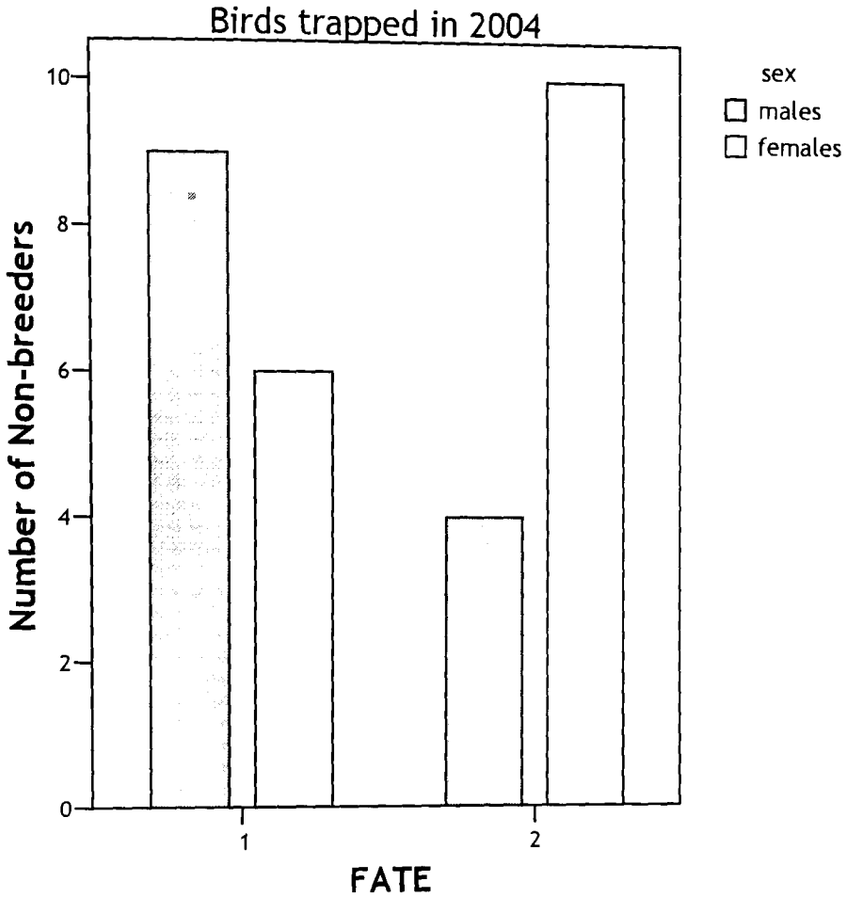


Figure 5.2: Number of male and female Non-breeding great skuas caught on Foula in 2004 and their fate in the following year (1=seen, 2=not seen).

5.3.3 Relationship between Fate and Body Condition

There were no differences in body condition between males and females in each year (2003: t=0.56, p=0.57, d.f. =40; 2004: t=0.30, p=0.76, d.f. =27). However, there was a significant difference in body condition between non-breeders trapped in 2003 and non-breeding birds trapped in 2004; in 2004 club birds were in better condition than in 2003 (F=4.8 d.f.=1,69 p=0.03, Table 5.1).

Table 5.1: Body Condition of non-breeding birds trapped on club sites in Foula.

year	N	Mean	s. d.
2003	42	-0.206	0.99
2004	29	0.298	0.89

Non-breeding birds that were seen in the colony again the year after they were trapped appeared to be in better condition than birds for which fate was unknown, re-sighted birds in 2003-04 had on average higher values of the body mass index in comparison to birds which were not seen either in club sites or territories (Figures 5.3 and 5.4). This tendency was not statistically significant (ANOVA: $F_{1,70}=2.01$, $p=0.16$, $N=71$). Body size was included as covariate in a previous model, but the relationship was not significant ($F_{1,70}=0.96$, $p=0.32$) therefore it was dropped from the final model. There were yearly differences in body condition, non-breeding birds trapped in 2004 were in better condition that non-breeders caught in 2003 (see 5.3.3).

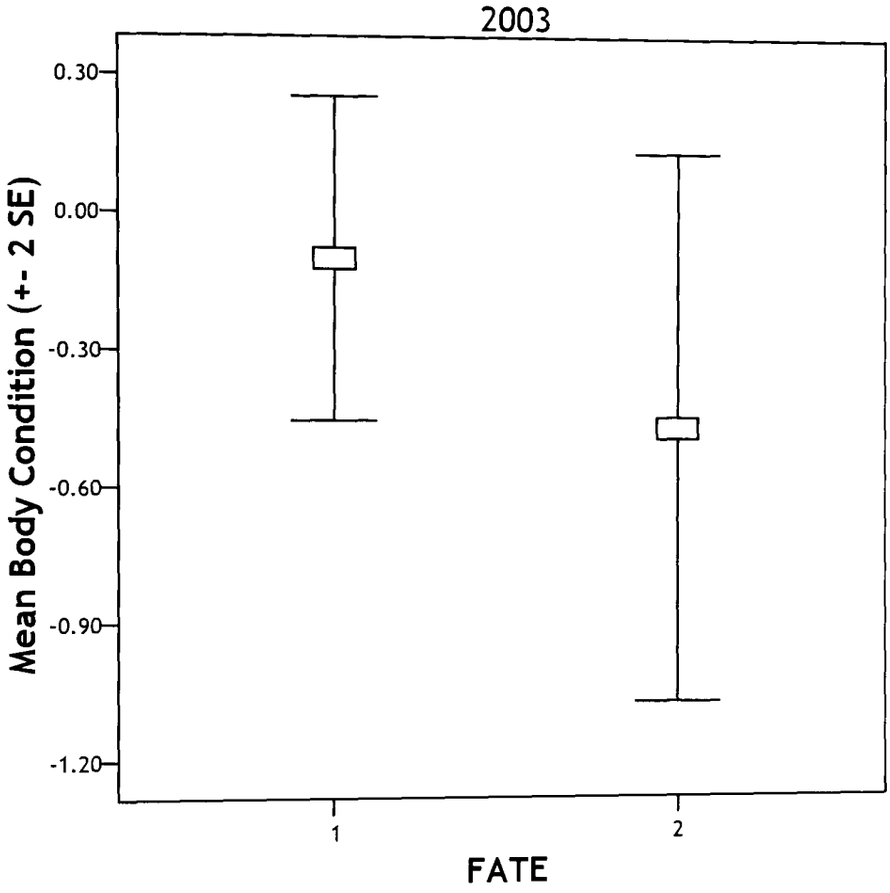


Figure 5.3: Mean Body Condition (± standard error*2) of Non-breeding birds trapped in clubs during 2003 and their FATE (1=seen, 2=not seen) on the subsequent year. Mean of known fate birds (±s.d.)= -0.100±0.96, N=30. Mean of unknown fate birds (±s.d.)=-0.471±1.04, N=12.

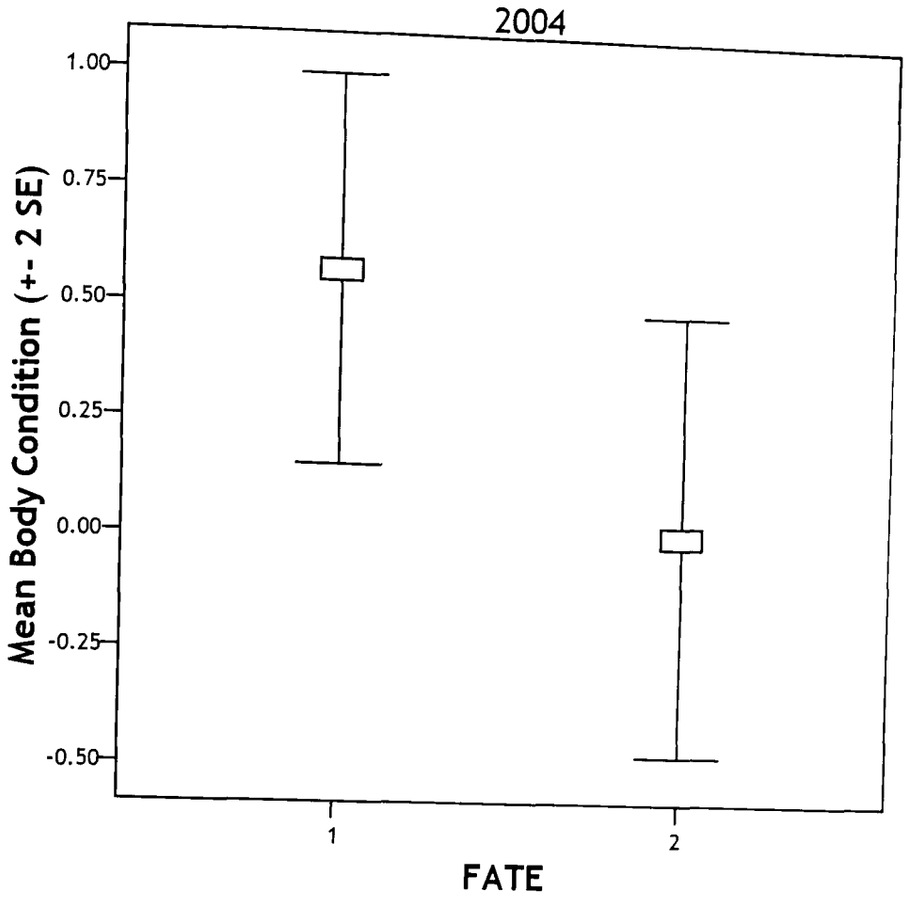


Figure 5.4: Mean Body Condition (± standard error*2) of Non-breeding birds trapped in clubs during 2004 and their FATE (1=seen, 2=not seen) on the subsequent year. Mean of known fate birds (±s.d.)= 0.573 ± 0.81, N=15. Mean of unknown fate birds (±s.d.)= 0.004 ± 0.90, N=14.

5.3.4 Status of Non-breeding birds one year after trapped in club sites.

Difference in Status was not related to sex, male and female prospectors were seen holding territories or in club sites in equal proportions (x^2=0.04, p=0.84). From all the birds trapped in both years, 35.2% of them were holding territories the following year. Four birds seen in club sites a year after being trapped were seen holding territories two years on. However six birds that were previously holding territories were not seen again at the colony in the second year of study (Table 5.2, see also Appendix 5.1).

Table 5.2: Non-breeding birds caught on club sites in Foula during the 2003 and 2004 breeding seasons and their status in 2004 and 2005.

NON BREEDERS	No. of birds trapped	STATUS subsequent year	STATUS two years after trapped
2003	42	14 back in club	2 in clubs
		16 holding territory	14 in territories/4 new "recruits"*
		12 unknown	26 unknown
2004	29	6 back in club	
		9 holding territory	
		14 unknown	

* new "recruits" means birds that were seen in club sites during 2004 and were holding territories in 2005.

5.3.5 Relationship between Body Condition and Status of Non-breeders.

The average body condition (BMI) of non-breeders that gained a territory during both years (2003-04) was similar to that of birds who remained in club sites [mean body condition (±s.d.) of territory holders =0.203±0.91, N=25 and club birds =0.024±1.03, N=20]. However, these differences were not statistically significant (ANOVA: $F_{1,43}$=0.38, p=0.54, N=45). In a previous model body size was included as covariate but the relationship was not significant ($F_{1,43}$=0.89, p=0.35) therefore it was not included in the final model. Yearly differences in body condition were found between birds that gained a territory and birds in club-sites, because birds were on average in better condition during 2003 than in 2004 (see 5.3.3).

When analyzed per year, birds that were holding a territory had on average higher body condition values than birds that returned to club sites, but these differences were not statistically significant (Figures 5.5 and 5.6).

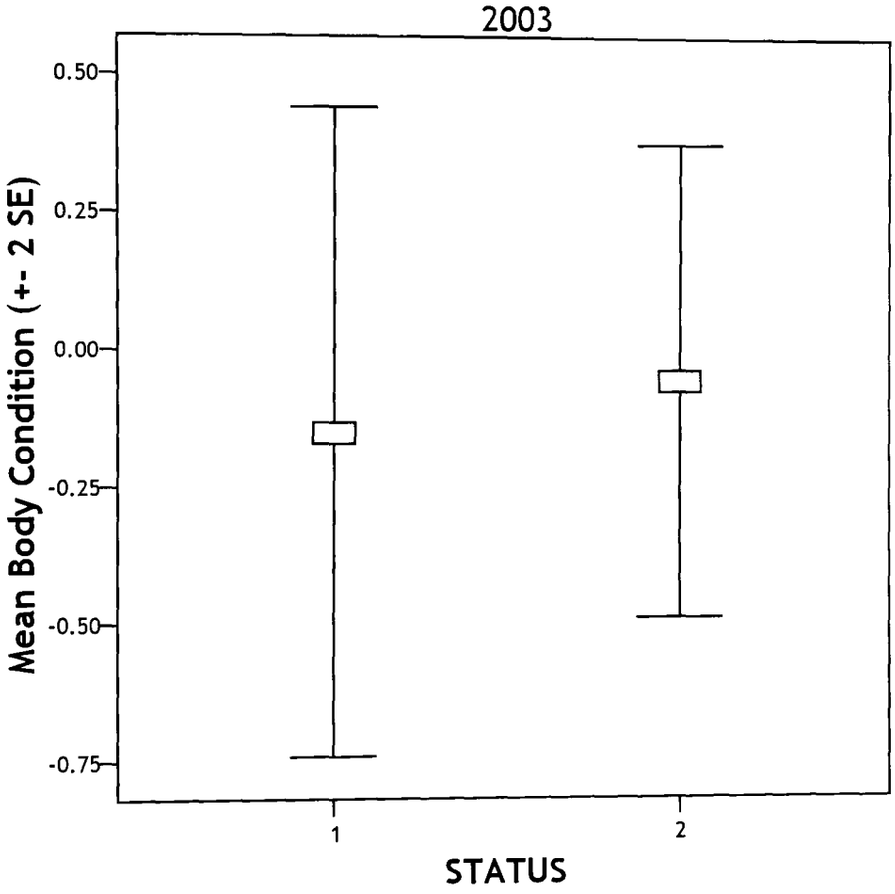


Figure 5.5: Mean Body Condition (± standard error*2) of Non-breeding birds trapped in clubs during 2003 and their STATUS (1=club, 2=territory) in the subsequent year. Mean of club birds (±s.d.)= -0.150 ± 1.10, N=14. Mean of territory holders (±s.d.)= -0.056 ± 0.86, N=16; t=0.26, d.f.=28, p=0.79.

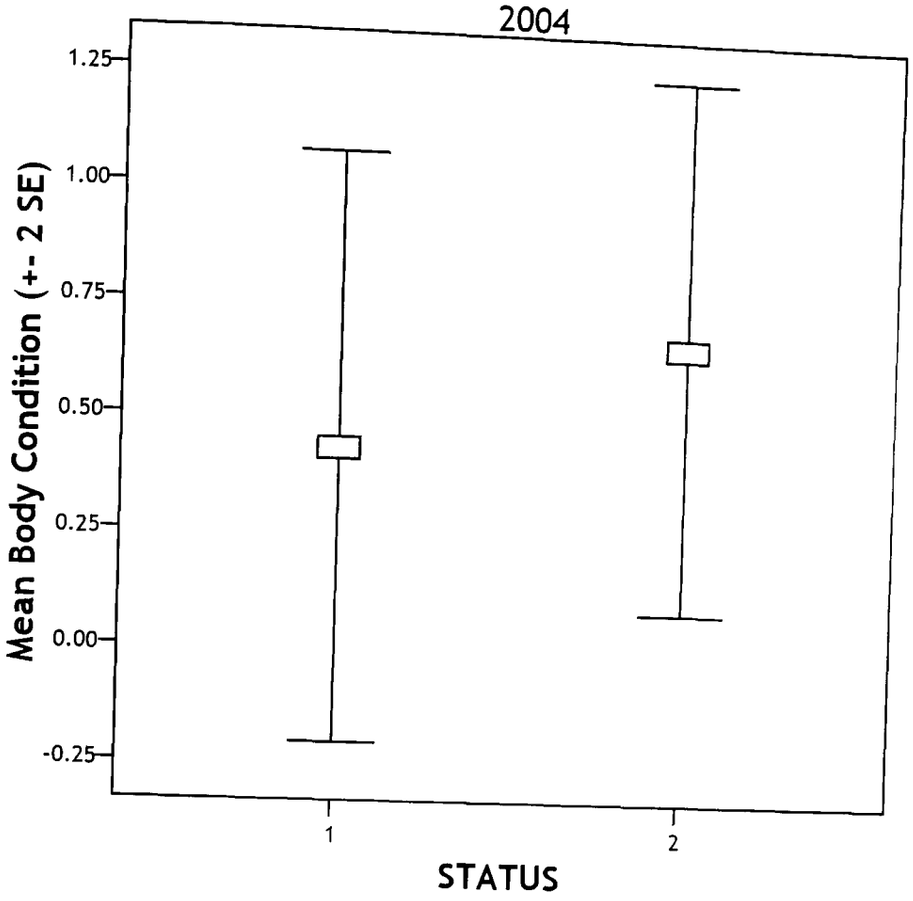


Figure 5.6: Mean Body Condition (± standard error*2) of Non-breeding birds trapped in clubs during 2004 and their STATUS (1=club, 2=territory) on the subsequent year. Mean of club birds (±s.d.)= 0.433 ± 0.78, N=6. Mean of territory holders (±s.d.)= 0.666 ± 0.87, N=9; t=0.52, d.f.=13, p=0.60.

5.4 DISCUSSION

It is clear that the major impact on the behaviour of non-breeding birds was seasonal differences. Although males' return rate remained almost unchanged from one year of study to the other (62.5% in 2004 and 69.2% in 2005), female return rate dropped from 83.3% to 37.5% from one season to the next. It is important to place these changes in the environmental context of the colony. An intriguing result was the average differences in body condition between the two seasons; non-breeders were in better body condition in 2004 compared to the values of 2003. In an attempt to find a possible explanation for this result, I looked at environmental factors such as food availability, climate change (NAO winter index) and breeding

success. First of all, the major source of food for great skuas is sandeel; the total sandeel biomass reported for the region dropped significantly from 2002 to 2003 and it was lower again in 2004 (see Table 2.1 in Chapter 2), so whereas this could be an explanation for low body condition in 2003, it leaves the question about the increase in body condition for 2004. Great skuas also rely on fisheries discards and are able to exploit other food sources (Votier 2004c), therefore they could be compensating for the lack of sandeel with a variation in their diet. Another environmental variable related to body condition is climate variation. The North Atlantic Oscillation (NAO) index has been related to bird's (and other vertebrates) performance in recent years (Durant et al. 2004; Grosbois and Thompson 2005). A positive value of the winter NAO usually corresponds to wetter and warmer weather in the northern seas and a negative value indicates the opposite (Hurrell 1995). Some studies have reported negative correlations between the NAO and survival of seabirds (Grosbois and Thompson 2005) however another study shows that return to the colony is associated with higher values of this index (Crespin et al. 2006). The value of the winter NAO (which corresponds to the months of December to March) for 2003 (positive) was higher than for 2004 (negative). This period of time is just before the return of the birds to the colony for the breeding season, but does not necessarily inform about the conditions faced during migration. A further look into the relationship between changing climate conditions and fish abundance in the region may give a clue of the effect on seabird body condition, yet the changes seen here from one season to the next may not be as dramatic and future longer periods of time need to be analysed in order to report a correlation.

Breeding success rate may be a sign of environmental conditions experienced by birds in the colony, in adverse circumstances one would expect a low rate, and the opposite when the situation improves. In 2003, the proportion of chicks per pair raised in the colony was 0.1, a major decrease from the previous year (2002= 0.6) but in 2004 productivity dropped dramatically to only 0.01 chicks per pair (see Table 2.1 in Chapter

2). Finding an explanation for the differences in body condition of non-breeders from one year to the next based on these data proves to be challenging. The reason why non-breeders appeared to be in higher body condition during 2004 may be an effect of the situation they faced during migration, or on arrival at the breeding site, allowing only fitter individuals to come back to the colony; in fact during 2004 colony attendance was reduced, fewer individuals were seen at clubs (see Chapter 4) and many known breeders were missing from their territories (pers. obs.), so it could be possible that only individuals in good condition were able to return to Foula for the breeding season, whilst the previous year when more birds were attending the colony, the variation in body condition was greater.

Body condition may be an important factor that determines non-breeders' fate from one season to the next. The results show a tendency in the difference between birds that returned to the colony and birds for which fate is unknown. Young seabirds usually return to their natal colony at the age of 2, and they attend club-sites for several years until they recruit to the breeding population (Nelson 1980; Furness and Monaghan 1987). However if there is strong competition for breeding space the assumption would be that only individuals in better condition would be able to gain a territory, leaving birds of lower condition with the decision of emigrating or remaining on clubs. Birds who returned to the Foula colony tended to be in better condition than birds which did not survive or may have emigrated to another colony.

Initially, the aim of this study was to investigate the factors affecting recruitment in the great skua at the Foula colony, however due to the unfavourable conditions experienced by the population no breeding of recruits was recorded (i.e. non of the marked non-breeders was seen to have laid eggs). So in this study the variable "recruitment" in fact refers to birds holding a territory amongst known breeders' territories. In total, 35.2% of prospectors (non-breeders trapped in club sites) were seen holding a territory in the next season. Although birds holding territories have slightly higher values of the body condition index than birds attending club sites, this difference was not statistically significant. It has been suggested

in the past that body condition is a prerequisite for recruitment and that recruits are in better condition than prospectors (Porter 1988). This might be the case in Foula but it is not strongly supported by the results.

As mentioned before (Chapter 2), the breeding success had been severely reduced in the last years. Actually the rate recorded in 2004 was the lowest for 30 years. This resulted in the conditions for recruitment being even less favourable than we had anticipated at the start of this research. Although in previous years the amount of sandeels and discards as well as the reproductive rate had declined, the numbers in 2004 were even lower. Some hypotheses associated to the process of recruitment state that prospectors would be attracted to colonies with high levels of attendance and with high breeding success (Boulinier et al. 1996; Boulinier and Danchin 1997; Danchin et al. 1998). Under the circumstances experienced in Foula, it was expected to find no recruitment at all to the colony as well as low attendance by both non-breeders and breeders. Non-breeders gaining territories could be a consequence of breeders leaving empty spaces therefore reducing the level of competition in the colony, but that did not signify that they were able to recruit (i.e. breed). In 2005 there were four new "recruits" in the colony but also six birds had dropped their gained territories; a likely suggestion is that prospectors have gone to surrounding colonies where conditions may be better for breeding. Other colonies in the Shetland region, especially some of the smaller colonies, reported higher breeding success than Foula (Mavor et al. 2006) and may be more attractive for potential recruits. Although there are no similar data to compare recruitment rates of previous years, the present study provides evidence that can be useful in future research of new breeders in the colony.

Measuring body condition can be subject to some variability, for practical reasons it is not always possible to trap all birds and obtain body measurements at the same time, I acquired a sample distributed along the breeding season. It would be ideal to acquire data at the beginning of the season to reduce any effect of seasonality in the body condition of the birds. Also different parameters that reflect quality of an individual should be consider, for known birds measures such as hatching date (see also

Chapter 3) and date of arrival at the colony. Also, the present study could be complemented with data from other colonies; a comparison between non-breeders from Foula and non-breeders from smaller colonies around Shetland could give evidence of the challenges (competition for space and food) faced by the birds. Additionally, having a bigger sample size would increment the probabilities of observing birds recruiting (breeding for the first time) and visiting surrounding colonies in search for marked individuals would provide evidence of the choices made by prospectors for a place to recruit.

Recruitment rates are major determinants of population size and reflect the status of the colonies (Oro and Pradel 2000). The Foula colony is the biggest colony of great skuas in the world, after a rapid growth in the number of breeding pairs during the late 1970s and the 1980s, the population started to decline; recently the numbers have not changed substantially which may indicate that the population has reached its carrying capacity (Furness and Ratcliffe 2004). Under this assumption it is possible to predict low recruitment rates for the future in Foula and an increase in the population of surrounding colonies, even the appearance of new colonies. As mentioned before, it would be very interesting to compare the body condition of prospectors between smaller colonies and Foula, we could expect to find that non-breeders in Foula need to be in better body condition than individuals attempting to breed in less competitive colonies.

Appendix 5.1: Non-breeders trapped in club sites in Foula.

Birds caught in 2003

COLOUR RING	CLUB NAME	FATE 2004	FATE 2005
LOSB	Strem Ness	club	Club
LOSO	Netherfandal	club	Club
LOOG	Netherfandal	club	Territory
LYWB	Netherfandal	club	Territory
LOOR	Strem Ness	club	Territory
LYWR	Strem Ness	club	Territory
LOOW	Netherfandal	territory	Territory
LOWO	Netherfandal	territory	Territory
LOOB	Strem Ness	territory	territory
LOYB	Strem Ness	territory	territory
LOBO	Strem Ness	territory	territory
LOBR	Strem Ness	territory	territory
LORB	Strem Ness	territory	territory
LOSW	Strem Ness	territory	territory
LOSY	Strem Ness	territory	territory
LOWS	Strem Ness	territory	territory
LOOS	Netherfandal	club	unknown
LORO	Netherfandal	club	unknown
LOWY	Netherfandal	club	unknown
LOYW	Netherfandal	club	unknown
LRSW	Netherfandal	club	unknown
LYWG	Netherfandal	club	unknown
LOOY	Strem Ness	club	unknown
LYRO	Strem Ness	club	unknown
LOBY	Netherfandal	territory	unknown
LORY	Strem Ness	territory	unknown
LOSR	Strem Ness	territory	unknown
LOWG	Strem Ness	territory	unknown
LOYO	Strem Ness	territory	unknown
LOYS	Strem Ness	territory	unknown
LORS	Netherfandal	unknown	unknown
LOSG	Netherfandal	unknown	unknown
LOWR	Netherfandal	unknown	unknown
LOYG	Netherfandal	unknown	unknown
LRBW	Netherfandal	unknown	unknown
LRGS	Netherfandal	unknown	unknown
LYWO	Netherfandal	unknown	unknown
LYWS	Netherfandal	unknown	unknown
LYWY	Netherfandal	unknown	unknown
LORG	Strem Ness	unknown	unknown
LORW	Strem Ness	unknown	unknown
LOYR	Strem Ness	unknown	unknown

Birds caught in 2004

COLOUR RING	CLUB NAME	FATE 2005
TYSB	Netherfandal	club
TYYO	Netherfandal	club
LORR	Strem Ness	club
LOWB	Strem Ness	club
TYBS	Strem Ness	club
TYWB	Strem Ness	club
TYBR	East Coast	territory
TYSS	Netherfandal	territory
TYST	Netherfandal	territory
TYSW	Netherfandal	territory
TYWR	Netherfandal	territory
TYWY	Netherfandal	territory
LOBS	Strem Ness	territory
LORB	Strem Ness	territory
TYSY	Strem Ness	territory
TYSR	Netherfandal	unknown
TYWT	Netherfandal	unknown
TYWW	Netherfandal	unknown
TYYR	Netherfandal	unknown
TYYS	Netherfandal	unknown
TYYW	Netherfandal	unknown
TYYY	Netherfandal	unknown
LOSS	Strem Ness	unknown
LOWW	Strem Ness	unknown
LOYY	Strem Ness	unknown
TYBB	Strem Ness	unknown
TYSO	Strem Ness	unknown
TYWO	Strem Ness	unknown
TYWS	Strem Ness	unknown

6. General Discussion

Studies about recruitment are very important in understanding population dynamics, and they are a valuable resource when studying seabird ecology. The recruitment rate is affected by environmental factors such as climate change (Crespin et al. 2006), space availability and colony density (Oro and Pradel 2000), and food supply (Spear et al. 1998); but it is also related to individual traits such as age (Prevot-Julliard et al. 2001) and body condition (Porter 1987). Along the course of this project it was interesting to see how some of these elements interacted in a high density colony. In recent years climate change studies have become increasingly frequent, not only for environmental reasons but for the effect the change in weather is having on animal behaviour and especially on breeding success (Barbraud and Weimerskirch 2003; Sanz 2003; Crick 2004). Although in this study the variable used to quantify climate change (NAO winter index) did not have a direct effect on reproductive variables (i.e. hatching date) or recruitment, climate change could affect individuals at other levels, for example it could be linked to food abundance and distribution in their breeding grounds and during their migration. Food availability is closely linked with individual performance, fish abundance has been widely related to seabird reproductive success, in many species there is a reduction in breeding success when sandeel abundance is low (Danchin 1992; Hamer et al. 1993; Phillips et al. 1996; Wanless et al. 2005). In great skuas, food abundance was related to reproductive success, early hatching and recruitment (see chapter 2). Great skuas' main food source is the lesser sandeel (*Ammodytes marinus*) while another important component of their diet is provided by fisheries discards (Hamer et al. 1991; Votier et al. 2001). Even though the effects of the NAO were not significant in this study, if the weather continues to change dramatically it could be possible to see an impact in the recruitment rates and breeding success of the colony in further seasons due to a reduction in food availability. In particular, it is thought that sandeel recruitment is adversely affected by higher sea temperatures (Arnott and Ruxton 2002). Furthermore, changes in fisheries' management could also impact seabird population dynamics (Furness 2002).

Analyses of 30 years of data in the Foula colony show that apart from the reduction in the number of breeding pairs, there is also a decline in the reproductive success of the colony, as it was shown in Chapter 2, these events are possibly related to a decline in both sandeel and fisheries discard abundance. At the same time, hatch date was also related to these variables, it was negatively related to breeding success and to sandeel abundance. Likewise, hatching date is correlated with recruitment age (Prevot-Julliard et al. 2001), therefore the limitation in resources for birds may transform into longer periods of non-breeding.

One of the most important aspects of the fieldwork conducted for this study was to individually mark non-breeders in order to follow their behaviour in subsequent years. The 2004 season proved to be challenging because the attendance of birds was very low compared to the previous year, number of birds present in club sites was comparatively less (Chapter 4) and many breeding territories were vacant. That year saw the lowest reproductive success in record for great skuas on Foula (Mavor et al. 2005), and also it was reported to have the lowest abundance of sandeel for the last three decades (see Table 2.1 in Chapter 2); and the same pattern was seen in other seabird colonies in the region (Mavor et al. 2005; Wanless et al. 2005). Therefore the chances of finding new recruits were minimal, yet I was able to find new birds holding territories and other marked individuals re-visiting the club sites. Under these limited circumstances (i.e. low food availability) it was difficult to expect new breeders to lay eggs, even if they were in good body condition; it could seem as if the only opportunity that prospectors had was to occupy empty territories of breeders that did not come back to the colony.

Although the situation improved in 2005 in terms of reproductive success (Mavor et al. 2006), colony attendance was still low and there was no recruitment, some prospectors were still holding territories but were unable to lay any eggs. During 2005, the data showed that a few individuals that had managed to obtain a territory in 2004 were not defending it anymore and were not even present in the colony (Chapter 5). If birds were

assessing the colony and its suitability for nesting in 2004, the outcome of the season must have discouraged them from attempting to breed there in 2005.

According to Porter (1988) one of the prerequisites for recruitment is body condition. In her study of kittiwakes she demonstrated that only high quality individuals would recruit to a colony. The results of the present study show something different (Chapter 3), non-breeders were in better condition than breeders. However, this was only the case for the most recent years (2003-2004) because in fact data from the 1970s and the 1980s show the opposite, concurring with previous ideas. The fact that in the recent environmental conditions breeders were in poorer condition than prospectors may also be evidence of density dependence effects happening on Foula, and cumulative costs of breeding effort being seen in breeders but not in immature birds.

The current situation in Foula is highly competitive and the only opportunities for new recruits seem to be empty spaces left by mortality of breeders. If indeed the colony has reached its carrying capacity, the alternative for birds looking to recruit is to emigrate to another colony. Data from surveys of the Foula colony show that in the past decade (1992-2002) the population numbers increased by only 5%, in contrast with other surrounding smaller colonies in Shetland with increases in numbers by 100% (Papa Stour) or even 650% (Whalsay); in fact almost all the other colonies in the Shetland region reported higher increases in the number of breeding pairs (Furness and Ratcliffe 2004). The Foula colony may still be attractive for native prospectors and even an alternative for foreign birds, but its current situation may prevent them from attempting to breed there.

The large variation in growth of the colonies around Shetland is related to human activity as well as other environmental variables. A good example is the island of Fair Isle, where the great skua colony (currently around 143 pairs) has failed to increase like in other similar colonies, due to persecution by islanders. During 2004 I visited the Fair Isle colony in an attempt to compare body condition of non-breeders subject to less competition, to birds in the densely populated Foula colony; this attempt

was unsuccessful due to low numbers of birds present, there were virtually no club birds and only a few breeders were nesting. In addition there was no colour ringed non-breeders from Foula suggesting that this colony was not suitable for prospectors in that season. Birds prospecting for a colony have other smaller growing colonies as alternatives in Shetland, or further south in Orkney and the north of Scotland.

The increase of the global population of great skuas occurred relatively recently, in the last century (Furness 1987; Furness and Ratcliffe 2004); in fact molecular analyses show that great skuas from Foula are not separated genetically from Icelandic birds (unpublished data, from analyses of mtDNA sequences by Kate Griffiths from blood samples collected by Bob Furness and colleagues). It is difficult to predict how far geographically the population could extend. It seems unlikely that they could colonize sites further south because of the differences in temperature (Furness 1987), and in fisheries activities (Furness and Ratcliffe 2004), but probably there is more opportunity to extend within the same or higher latitudes; already there are records of British birds moving to Russia.

Recently, studies of recruitment are being given a new approach by the use of capture-mark-recapture methods, in which individuals are captured, marked and released, and recapture at different stages in their lives (Pradel 1996). These models can determine the probabilities of being in a population before breeding for the first time, and they can have the input of other variables that could affect the process of recruitment at any stage (Pradel 1996; Pradel et al. 1997; Cam et al. 2003; Lebreton et al. 2003; Crespin et al. 2006). These analyses are very useful when there are long-term sets of data, in populations where many individuals have been followed all their lives, and they give information about factors affecting recruitment and the possibility of making predictions for such populations.

Klomp and Furness (1992) predicted a decline in the pool of potential recruits and of the breeding numbers in Foula from the 1990s, also they suggested that monitoring the number of non-breeders in the colony could provide warnings of the environmental stress affecting the population; the

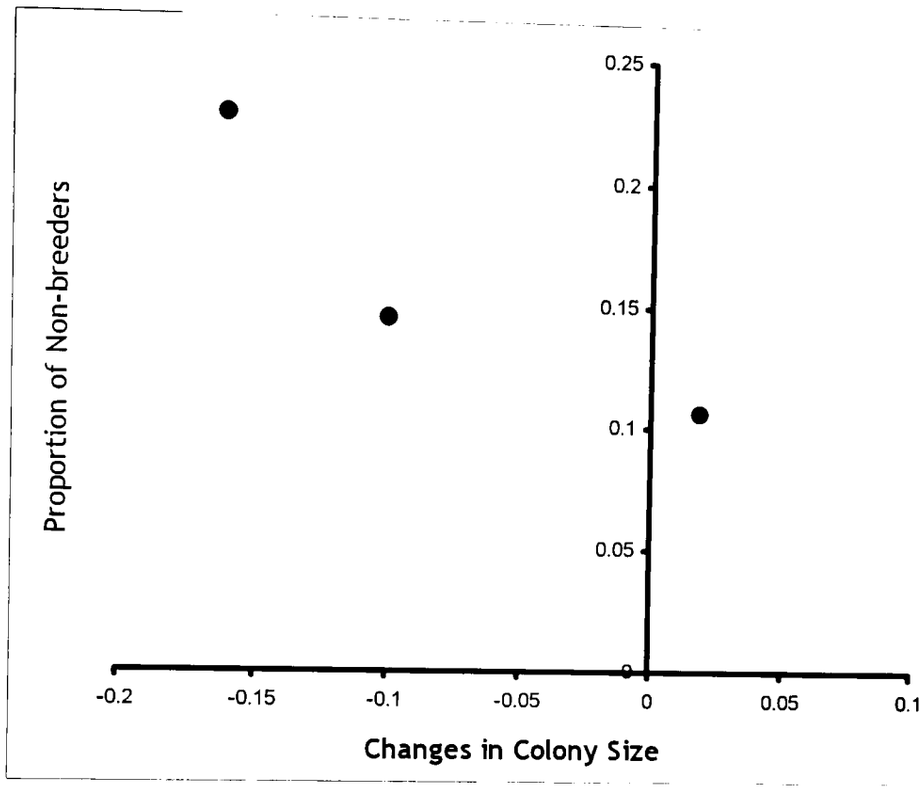
present study supports these ideas by showing lower numbers of potential recruits correlated with a limitation of resources in the colony. Also, I agree that in the case of the great skua colony in Foula, non-breeders are acting as indicators of the health of the population (Porter and Coulson 1987).

Combining the data obtained previously of the number of non-breeders in Foula and the colony size (AOTs), and the observations of this study in a model (Appendix 6.1), it is possible to see how numbers of breeders could be related to the number of prospectors. Also, this shows that from the first decade of counts a notable drop in the number of non-breeders coincided with a larger decline in the colony size, in the next two decades the change was not as prominent. It would be possible to predict that the number of non-breeders (and thus the colony size) would continue to decline until it reaches the point of sustainability; whilst approaching this point, changes would be smaller year after year. Likewise, if the situation in the colony improved in terms of food availability numbers would be on the rise.

The size of the "pool of potential recruits" could also be assessed by estimating the number of unmarked birds attending the club-sites in relation to the number of marked individuals. So, the observer would be confident that obtaining a precise measure of known individuals could signify a reliable approximation of the non-breeding population.

In sum, the current situation in Foula regarding density, competition and food availability has a strong impact on recruitment rates; it is possible that in the next years recruitment would be minimal. Alternatively, smaller colonies around Shetland may see an increase in their breeding numbers. It would be very interesting to find birds born in Foula recruiting into other colonies, as this suggests that the rate of emigration from the Foula colony must have increased substantially over recent years. Studies like the one presented in this thesis provide valuable information for conservation plans and contribute to the understanding of the factors intervening in the regulation of seabird populations.

Appendix 6.1: Colony size and Number of Non-breeders.



Appendix 6.1: Colony size (AOTs) and Proportion of Non-breeders (non-breeders/breeders) present in the colony during surveys. Colony size data corresponds to the decrease/increase in numbers of AOTs from 1977 to 1986, 1986 to 1999 and 1999 to 2000 (actual survey counts see Chapter 2, Figure 2.1) and counts of non-breeders done in 1986, 1988 and 2003 (present study, see Chapter 4, Figure 4.3).

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